GENERAL ECOLOGY



Tara Jo Holmberg
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General Ecology

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TEAM - PA Ecology

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CHAPTER OVERVIEW

Chapter 0: The Study of Life

0.1: Themes and Concepts of Biology

0.2: The Nature of Science

0.3: The Role of Science in Society

1.E: The Study of Life (Exercises)

Thumbnail: A cluster of Escherichia coli bacteria magnified 10,000 times. (Public Domain; Eric Erbe, digital colorization by Christopher Pooley, both of USDA, ARS, EMU).

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Themes and Concepts of Biology

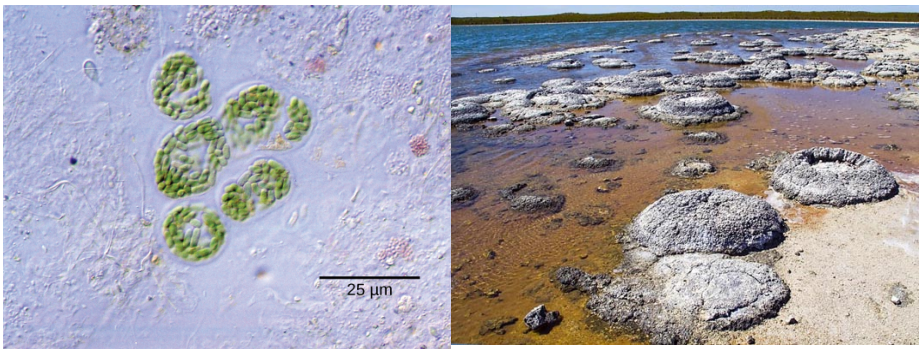
- Please read and watch the following Mandatory Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 1 hour.
- Optional Activities and Resources are embedded.
- To navigate to the next Section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Identify and describe the properties of life
- Describe the levels of organization among living things
- Identify the shared characteristics of the natural sciences
- Identify examples of different subdisciplines in biology

What is Biology?

In simple terms, biology is the study of living organisms and their interactions with one another and their environments. This is a very broad definition because the scope of biology is vast. Biologists may study anything from the microscopic or submicroscopic view of a cell to ecosystems and the whole living planet (Figure 0.1.1).



(a) (b)

Figure 0.1.1: Formerly called blue-green algae, these (a) cyanobacteria, shown here at 300x magnification under a light microscope, are some of Earth's oldest life forms. These (b) stromatolites along the shores of Lake Thetis in Western Australia are ancient structures formed by the layering of cyanobacteria in shallow waters. (credit a: modification of work by NASA; credit b: modification of work by Ruth Ellison; scale-bar data from Matt Russell)

Listening to the daily news, you will quickly realize how many aspects of biology are discussed every day. For example, recent news topics include *Escherichia coli* (Figure 0.1.2) outbreaks in spinach and *Salmonella* contamination in peanut butter. Other subjects include efforts toward finding a cure for AIDS, Alzheimer's disease, and cancer. On a global scale, many researchers are committed to finding ways to protect the planet, solve environmental issues, and reduce the effects of climate change. All of these diverse endeavors are related to different facets of the discipline of biology.

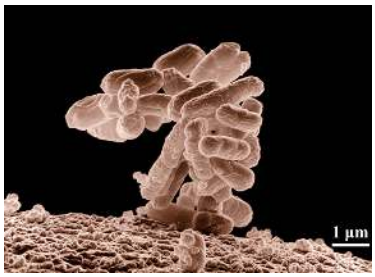


Figure 0.1.2: *Escherichia coli* (*E. coli*) bacteria, seen in this scanning electron micrograph, are normal residents of our digestive tracts that aid in the absorption of vitamin K and other nutrients. However, virulent strains are sometimes responsible for disease outbreaks. (credit: Eric Erbe, digital colorization by Christopher Pooley, both of USDA, ARS, EMU)

Optional Resource

Find an example of up-to-date news on biology at Science Daily here: https://www.sciencedaily.com/news/plants_animals/biology/

Biology is the science that studies life, but what exactly is life? This may sound like a silly question with an obvious response, but it is not always easy to define life. For example, a branch of biology called **virology** studies viruses, which exhibit some of the characteristics of living entities but lack others. It turns out that although viruses can attack living organisms, cause diseases, and even reproduce, they do not meet the criteria that biologists use to define life. Consequently, virologists are not biologists, strictly speaking. Similarly, some biologists study the early molecular evolution that gave rise to life; since the events that preceded life are not biological events, these scientists are also excluded from biology in the strict sense of the term.

From its earliest beginnings, biology has wrestled with three questions:

1. What are the shared properties that make something “alive”?
2. And once we know something is alive, how do we find meaningful levels of organization in its structure?
3. And, finally, when faced with the remarkable diversity of life, how do we organize the different kinds of organisms so that we can better understand them?

As new organisms are discovered every day, biologists continue to seek answers to these and other questions.

Video





Watch this 1.5-minute video as multiple scientists and professors describe what biology means to them.
Question after watching:
What does biology mean to you?

Properties of Life

All living organisms share several key characteristics or functions: order, sensitivity or response to the environment, reproduction, adaptation, growth and development, regulation, homeostasis, energy processing, and evolution. When viewed together, these are nine characteristics that can serve to define life. However, different scientists have used varying definitions to classify matter as living (**biotic**) or non-living (**abiotic**). Some use seven or fewer of these characteristics, some use all nine. One of the most concise definitions of life is from the National Aeronautics and Space Administration "*Life is a self-sustaining chemical system capable of Darwinian evolution*" (NASA, 2022).

Order

Organisms are highly organized, coordinated structures that consist of one or more cells. Even very simple, single-celled organisms are remarkably complex: inside each cell, atoms make up molecules; these, in turn, make up cell organelles and other cellular inclusions. In multicellular organisms (Figure 0.1.1), similar cells form tissues. Tissues, in turn, collaborate to create organs (body structures with a distinct function). Organs work together to form organ systems.



Figure 0.1.1: A toad represents a highly organized structure consisting of cells, tissues, organs, and organ systems. (credit: “Ivengo”/Wikimedia Commons)

Sensitivity or Response to Stimuli

Organisms respond to diverse stimuli. For example, plants can bend toward a source of light (**phototaxis**), climb on fences and walls, or respond to touch (Figure 0.1.2). Even tiny bacteria can move toward or away from chemicals (**chemotaxis**) or light.



Figure 0.1.2: The leaves of this sensitive plant (*Mimosa pudica*) will instantly droop and fold when touched. After a few minutes, the plant returns to normal. (credit: Alex Lomas)

Video



Watch this 1-minute video to see how plants respond to a stimulus (sunlight) and what that means for their success.

Question after watching:

What are other types of stimuli that the plant encounters?

Reproduction

Single-celled organisms reproduce by first duplicating their DNA, and then dividing it equally as the cell prepares to divide to form two new cells. Multicellular organisms often produce specialized reproductive germline cells, such as eggs and sperm, that will form new individuals. When reproduction occurs, genes containing DNA are passed along to an organism's offspring. These genes ensure that the offspring will belong to the same species and will have similar characteristics, such as size and shape.

Growth and Development

Organisms grow and develop following specific instructions coded for by their **genes**. These genes provide instructions that will direct cellular growth and development, ensuring that a species' young will grow up to exhibit many of the same characteristics as its parents (Figure 0.1.3).



Figure 0.1.3: Although no two look alike, these kittens have inherited genes from both parents and share many of the same characteristics. (credit: Rocky Mountain Feline Rescue)

Regulation

Even the smallest organisms are complex and require multiple regulatory mechanisms to coordinate internal functions, respond to stimuli, and cope with environmental stresses. Two examples of internal functions regulated in an organism are nutrient transport and blood flow. **Organs** (groups of tissues working together) perform specific functions, such as carrying oxygen throughout the body, removing wastes, delivering nutrients to every cell, and cooling the body.

Homeostasis

In order to function properly, cells need to have appropriate conditions such as proper temperature, pH, and appropriate concentration of diverse chemicals. These conditions may, however, change from one moment to the next. Organisms are able to maintain internal conditions within a narrow range almost constantly, despite environmental changes, through **homeostasis** (literally, "steady state")—the ability of an organism to maintain constant internal conditions.

For example, an organism needs to regulate body temperature through a process known as thermoregulation. Organisms that live in cold climates, such as the polar bear (Figure 0.1.4), have body structures that help them withstand low temperatures and conserve body heat. Structures that aid in this type of insulation include fur, feathers, blubber, and fat. In hot climates, organisms have methods (such as perspiration in humans or panting in dogs) that help them to shed excess body heat.



Figure 0.1.4: Polar bears (*Ursus maritimus*) and other mammals living in ice-covered regions maintain their body temperature by generating heat and reducing heat loss through thick fur and a dense layer of fat under their skin. (credit: "longhorndave"/Flickr)

Energy Processing

All organisms use a source of energy for their metabolic activities. Some organisms capture energy from the sun and convert it into chemical energy in food; others use chemical energy in molecules they take in as food (Figure 0.1.5).



Figure 0.1.5: The California condor (*Gymnogyps californianus*) uses chemical energy derived from food to power flight. California condors are an endangered species; this bird has a wing tag that helps biologists identify the individual. (credit: Pacific Southwest Region U.S. Fish and Wildlife Service)

Evolution

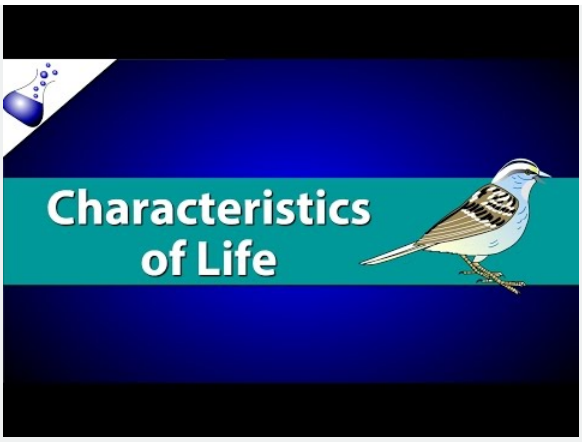
All organisms evolve. We will investigate the theory of evolution and its mechanisms thoroughly in Unit 2.

Videos


Seven Life Processes | Physiology | Biology | Fuse
FuseSchool - Global Education
Biology
SEVEN LIFE PROCESSES
Watch on YouTube


Biology
SEVEN LIFE PROCESSES


Characteristics of Life
RicochetScience
Characteristics of Life
Watch on YouTube



Use these two videos to help you synthesize the ideas from above about the processes of life.
Question after watching:
Which features help scientists separate the biotic from the abiotic?

Levels of Organization of Living Things

Living things are highly organized and structured, following a hierarchy that can be examined on a scale from small to large. The **atom** is the smallest and most fundamental unit of matter. It consists of a nucleus surrounded by electrons. Atoms form molecules. A **molecule** is a chemical structure consisting of at least two atoms held together by one or more chemical bonds. Many molecules that are biologically important are **macromolecules**, large molecules that are typically formed by polymerization (a polymer is a large molecule that is made by combining smaller units called monomers, which are simpler than macromolecules). An example of a macromolecule is deoxyribonucleic acid (DNA) (Figure 0.1.6), which contains the instructions for the structure and functioning of all living organisms.

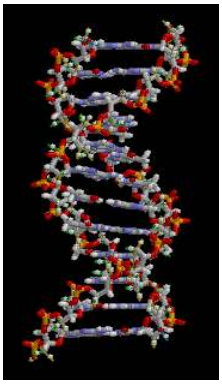


Figure 0.1.6: All molecules, including this DNA molecule, are composed of atoms. (credit: "brian0918"/Wikimedia Commons)

Some cells contain aggregates of macromolecules surrounded by membranes; these are called **organelles**. Organelles are small structures that exist within cells. Examples of organelles include mitochondria and chloroplasts, which carry out indispensable functions: mitochondria produce energy to power the cell, while chloroplasts enable green plants to utilize the energy in sunlight to make sugars. All living things are made of **cells**; the cell itself is the smallest fundamental unit of structure and function in living organisms. (This requirement is why viruses are not considered living: they are not made of cells. To make new viruses, they have to invade and hijack the reproductive mechanism of a living cell; only then can they obtain the materials they need to reproduce.) Some organisms consist of a single cell and others are multicellular. Cells are classified as **prokaryotic** or **eukaryotic**. Prokaryotes are single-celled or colonial organisms that do not have membrane-bound nuclei; in contrast, the cells of eukaryotes do have membrane-bound organelles and a membrane-bound nucleus.

In larger organisms, cells combine to make **tissues**, which are groups of similar cells carrying out similar or related functions. **Organs** are collections of tissues grouped together performing a common function. Organs are present not only in animals but also in plants. An **organ system** is a higher level of organization that consists of functionally related organs. Mammals have many organ systems. For instance, the circulatory system transports blood through the body and to and from the lungs; it includes organs such as the heart and blood vessels. **Organisms** are individual living entities. For example, each tree in a forest is an organism. Single-celled prokaryotes and single-celled eukaryotes are also considered organisms and are typically referred to as microorganisms.

All the individuals of a species living within a specific area are collectively called a **population**. For example, a forest may include many pine trees. All of these pine trees represent the population of pine trees in this forest. Different populations may live in the same specific area. For example, the forest with pine trees includes populations of flowering plants and also insects and microbial populations. A **community** is the sum of populations inhabiting a particular area. For instance, all of the trees, flowers, insects, and other populations in a forest form the forest's community. The forest itself is an **ecosystem**. An ecosystem consists of all the living things in a particular area together with the abiotic, non-living parts of that environment such as nitrogen in the soil or rainwater. At the highest level of organization, the **biosphere** is the collection of all ecosystems, and it represents the zones of life on earth (Figure 0.1.7). It includes land, water, and even the atmosphere to a certain extent.

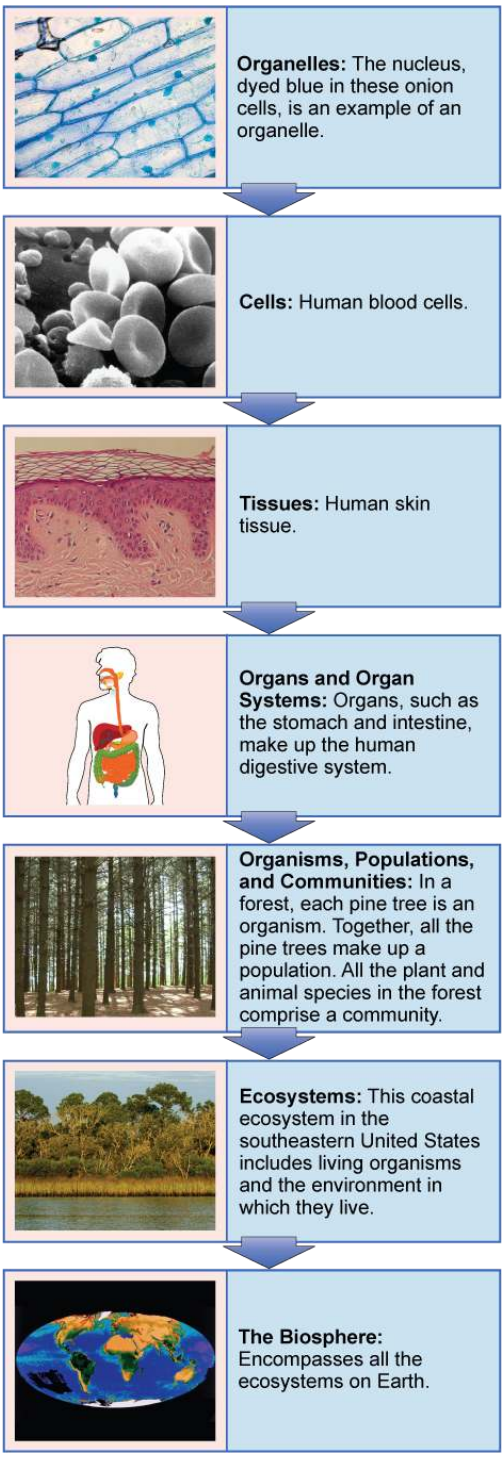
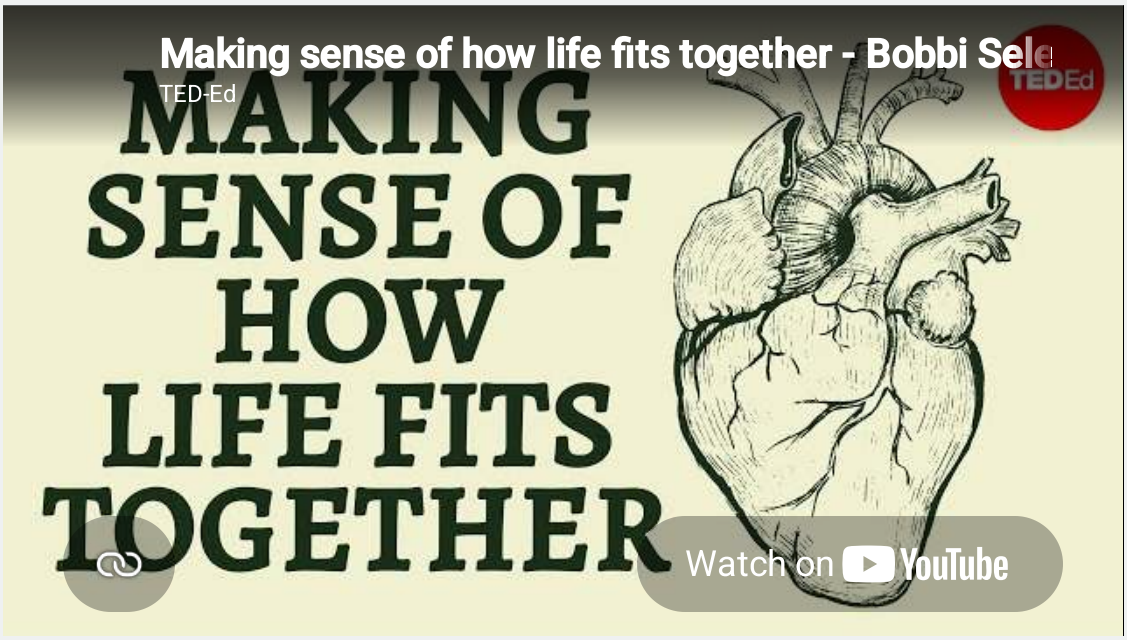
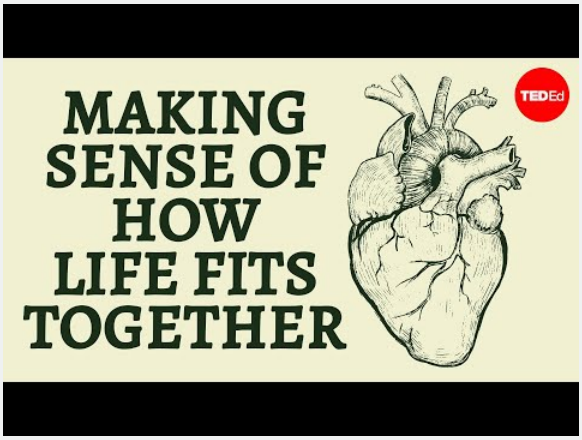


Figure 0.1.7: The biological levels of organization of living things are shown. From a single organelle to the entire biosphere, living organisms are parts of a highly structured hierarchy. (credit “organelles”: modification of work by Umberto Salvagnin; credit “cells”: modification of work by Bruce Wetzel, Harry Schaefer/ National Cancer Institute; credit “tissues”: modification of work by Kilbad; Fama Clamosa; Mikael Häggström; credit “organs”: modification of work by Mariana Ruiz Villareal; credit “organisms”: modification of work by "Crystal"/Flickr; credit “ecosystems”: modification of work by US Fish and Wildlife Service Headquarters; credit “biosphere”: modification of work by NASA)

Video





Discover the many different levels of organization of life in this 5-minute video.

Question after watching:

Many scientists specialize in a level of organization. If you were to study only one section of biological organization, which would you choose and why

Optional Activity 0.1.1

Which of the following statements is false? Refer to the text above for the correct answer.

A. Tissues exist within organs which exist within organ systems.
B. Communities exist within populations which exist within ecosystems.
C. Organelles exist within cells which exist within tissues.
D. Communities exist within ecosystems which exist in the biosphere.

Answer

B. Communities exist within populations which exist within ecosystems. This is an incorrect answer as populations ar least inclusive, then communities, then ecosystems.

The Diversity of Life

The fact that biology, as a science, has such a broad scope has to do with the tremendous diversity of life on earth. The source of this diversity is evolution, the process of gradual change during which new species arise from older species. Evolutionary biologists study the evolution of living things in everything from the microscopic world to ecosystems.

The evolution of various life forms on Earth can be summarized in a phylogenetic tree (Figure 0.1.8). A phylogenetic tree is a diagram showing the evolutionary relationships among biological species based on similarities and differences in genetic or physical traits or both. A phylogenetic tree is composed of nodes and branches. The internal nodes represent ancestors and are points in evolution when, based on scientific evidence, an ancestor is thought to have diverged to form two new species. The length of each branch is proportional to the time elapsed since the split.

We will investigate the diversity of life further in Unit 3.

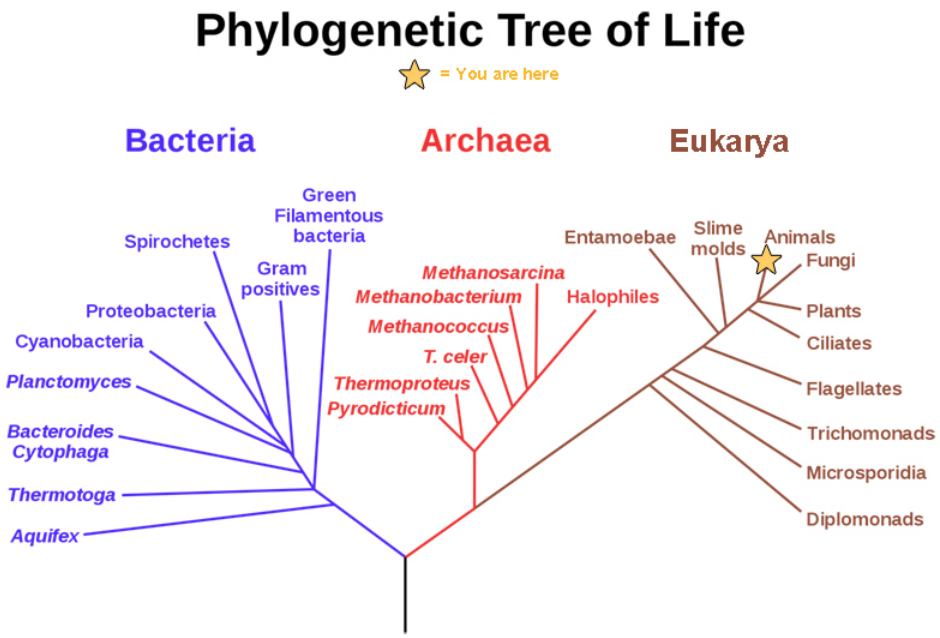


Figure 0.1.8: This phylogenetic tree was constructed by microbiologist Carl Woese using data obtained from sequencing ribosomal RNA genes. The tree shows the separation of living organisms into three domains: Bacteria, Archaea, and Eukarya. Bacteria and Archaea are prokaryotes, single-celled organisms lacking intracellular organelles. (credit: Eric Gaba; NASA Astrobiology Institute)

Evolution Connection: Carl Woese and the Phylogenetic Tree

In the past, biologists grouped living organisms into five kingdoms: animals, plants, fungi, protists, and bacteria. The organizational scheme was based mainly on physical features, as opposed to physiology, biochemistry, or molecular biology, all of which are used by modern systematics. The pioneering work of American microbiologist Carl Woese in the early 1970s has shown, however, that life on Earth has evolved along three lineages, now called domains—Bacteria, Archaea, and Eukarya. The first two are prokaryotic cells with microbes that lack membrane-enclosed nuclei and organelles. The third domain contains the eukaryotes and includes unicellular microorganisms together with the four original kingdoms (excluding bacteria). Woese defined Archaea as a new domain, and this resulted in a new taxonomic tree (Figure 0.1.8). Many organisms belonging to the Archaea domain live under extreme conditions and are called extremophiles. To construct his tree, Woese used genetic relationships rather than similarities based on morphology (shape).

Woese's tree was constructed from comparative sequencing of the genes that are universally distributed, present in every organism, and conserved (meaning that these genes have remained essentially unchanged throughout evolution). Woese's approach was revolutionary because comparisons of physical features are insufficient to differentiate between the prokaryotes that appear fairly similar in spite of their tremendous biochemical diversity and genetic variability (Figure 0.1.9). The

comparison of homologous DNA and RNA sequences provided Woese with a sensitive device that revealed the extensive variability of prokaryotes, and which justified the separation of the prokaryotes into two domains: bacteria and archaea.

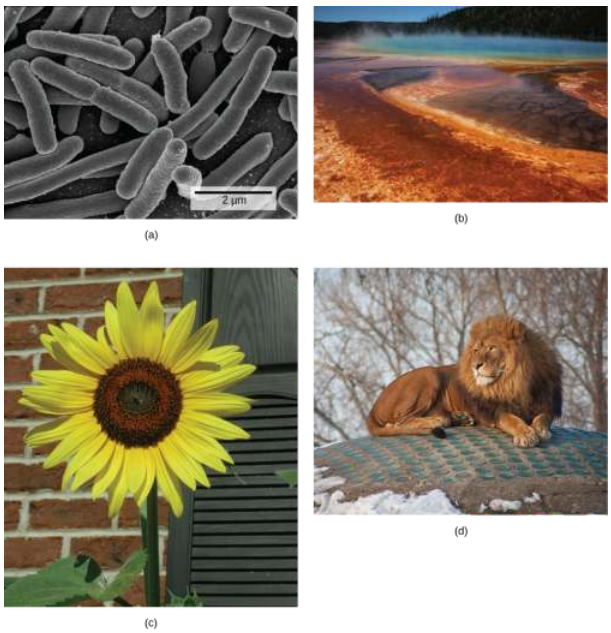
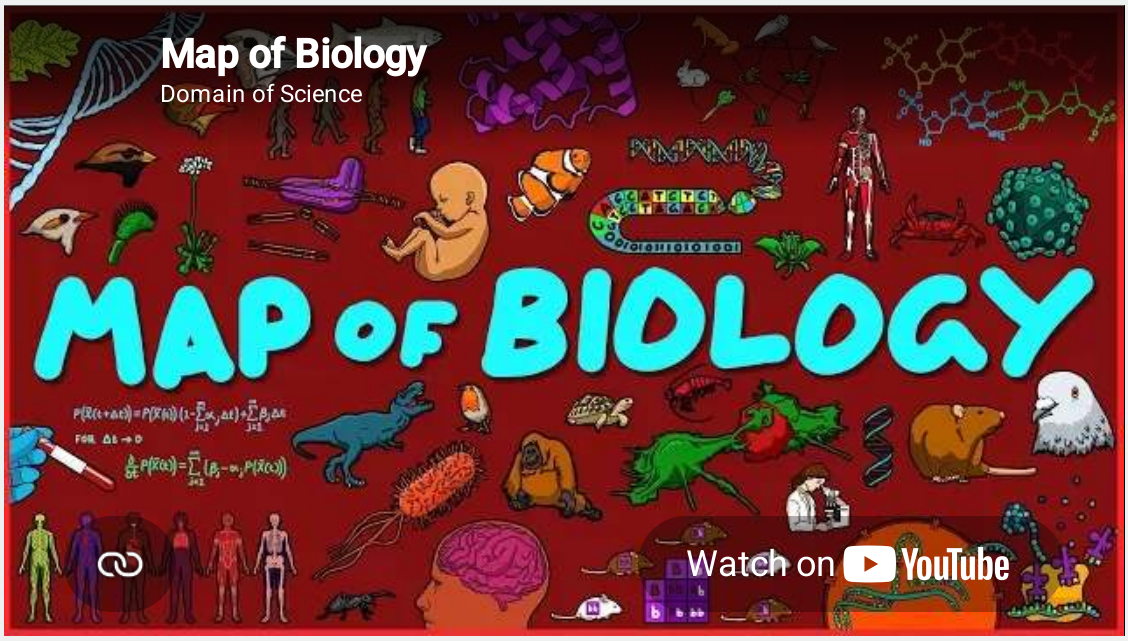


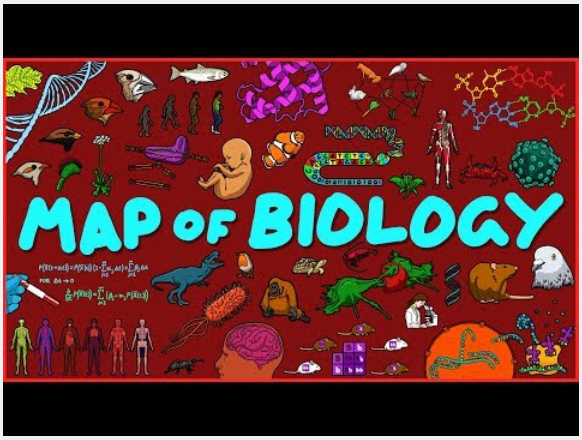
Figure 0.1.9: These images represent different domains. The (a) bacteria in this micrograph belong to Domain Bacteria, while the (b) extremophiles (not visible) living in this hot vent belong to Domain Archaea. Both the (c) sunflower and (d) lion are part of Domain Eukarya. (credit a: modification of work by Drew March; credit b: modification of work by Steve Jurvetson; credit c: modification of work by Michael Arrighi; credit d: modification of work by Leszek Leszcynski)

Branches of Biological Study

The scope of biology is broad and therefore contains many branches and subdisciplines. Biologists may pursue one of those subdisciplines and work in a more focused field. For instance, molecular biology and biochemistry study biological processes at the molecular and chemical level, including interactions among molecules such as DNA, RNA, and proteins, as well as the way they are regulated. Microbiology, the study of microorganisms, is the study of the structure and function of single-celled organisms. It is quite a broad branch on its own, and depending on the subject of study, there are also microbial physiologists, ecologists, and geneticists, among others.

Video





This 9-minute video describes many of the fields of biology.
Question after watching: Which of the fields are new to you?

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The Nature of Science

- Please read and watch the following Mandatory Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 2.5 hours.
- Optional Activities and Resources are embedded.
- To navigate to the next Section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Use strategies of scientific inquiry to evaluate information, problems, and the validity of science;
- Model the scientific method;
- Compare inductive reasoning with deductive reasoning;
- Compare and contrast observational and descriptive studies;

The Process of Science

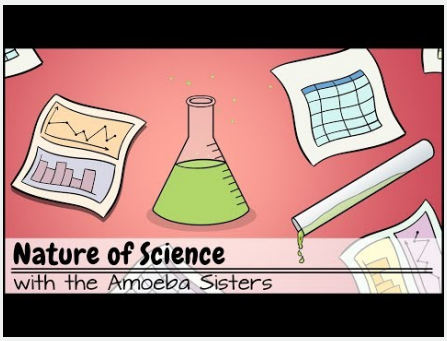
Biology is a science, but what exactly is science? What does the study of biology share with other scientific disciplines? **Science** (from the Latin *scientia*, meaning "knowledge") can be defined as a process that uses evidence, logic, and creativity to discover and explain natural and physical phenomenon while avoiding bias. The **scientific method** is a method of research with defined steps that include experiments and careful observation.

The steps of the scientific method will be examined in detail later, but one of the most important aspects of this method is the testing of hypotheses by means of repeatable experiments. A **hypothesis** is a suggested explanation for an event, which can be tested. Although using the scientific method is inherent to science, it is inadequate in determining what science is. It is relatively easy to apply the scientific method to disciplines such as physics and chemistry, but for disciplines like paleontology and geology, the scientific method is adapted to the field of study.

These areas of study are still sciences, however. Consider paleontology—even though one cannot perform repeatable experiments, hypotheses may still be supported. For instance, a paleontologist can hypothesize that an ancient organism existed based on finding a fossil. Further hypotheses could be made about various characteristics of this fossil, and these hypotheses may be found to be correct or false through continued support or contradictions from other findings. A hypothesis may become a theory with time and evidence. A **theory** is a well-tested and confirmed explanation for observations or phenomena. Science may be better defined as fields of study that attempt to comprehend the physical and natural underpinnings of the universe.

Video





This 10-minute video provides an overview of the process of science.
Question after watching: "What additional characteristics/steps has this video proposed is important in the scientific process that was not mentioned in the text above?"

Natural Sciences

What would you expect to see in a museum of natural sciences? Frogs? Plants? Dinosaur skeletons? Exhibits about how the brain functions? A planetarium? Gems and minerals? Or, maybe all of the above? Science includes such diverse fields as astronomy, biology, computer sciences, geology, logic, physics, chemistry, and mathematics (Figure 0.2.1). However, those fields of science related to the physical world and its phenomena and processes are considered **natural sciences**. Thus, a museum of natural sciences might contain any of the items listed above.

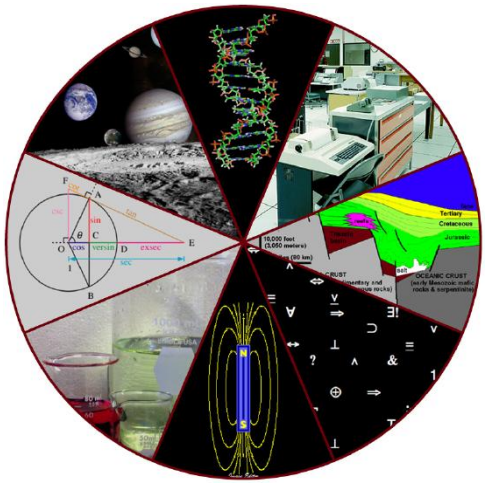
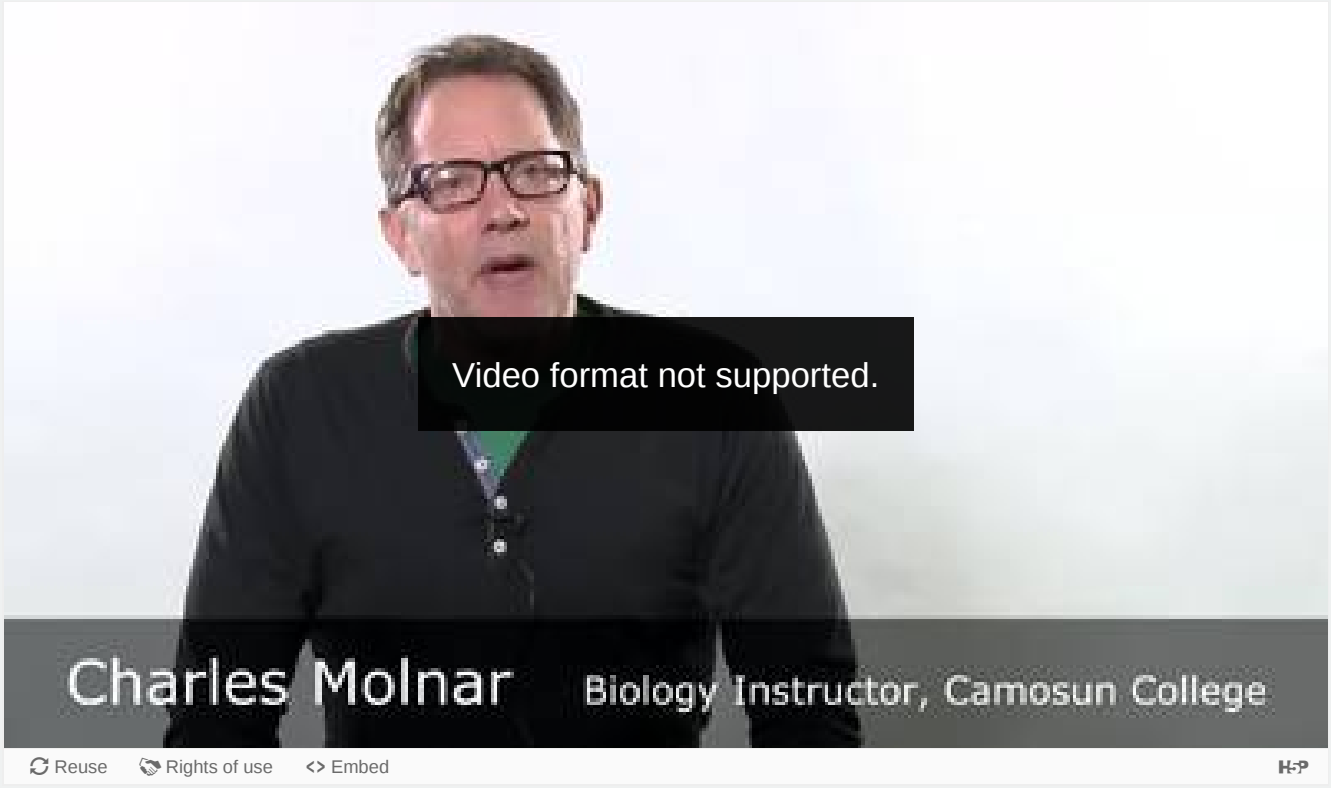


Figure 0.2.1: The diversity of scientific fields includes astronomy, biology, computer science, geology, logic, physics, chemistry, mathematics, and many other fields. (credit: “Image Editor”/Flickr)

There is no complete agreement when it comes to defining what the natural sciences include, however. For some experts, the natural sciences are astronomy, biology, chemistry, earth science, and physics. Other scholars choose to divide natural sciences into **life sciences**, which study living things and include biology, and **physical sciences**, which study nonliving matter and include astronomy, geology, physics, and chemistry. Some disciplines such as biophysics and biochemistry build on both life and physical sciences and are **interdisciplinary**. Natural sciences often rely on the use of **quantitative**, or numeric, data although some may use **qualitative**, or non-numeric, data to support findings.

Not surprisingly, the natural science of biology has many branches or **subdisciplines**. Cell biologists study cell structure and function, while biologists who study anatomy investigate the structure of an entire organism. Those biologists studying physiology, however, focus on the internal functioning of an organism. Some areas of biology focus on only particular types of living things. For example, botanists explore plants, while zoologists specialize in animals.

Video



This 5-minute video provides the purpose of the scientific method.
Question after watching: "Charles Molnar describes many ways in which human biases can influence how we observe or interpret the world around us. What steps do scientists put in place to try to remove these human biases from the process of learning about the world so that the final findings are as objective as possible?"

History of Biological Science

Although modern biology is a relatively recent development, sciences related to and included within it have been studied since ancient times. Natural philosophy was studied as early as the ancient civilizations of Mesopotamia, Egypt, the Indian subcontinent, and China. However, the origins of modern biology and its approach to the study of nature are most often traced back to ancient Greece. (Biology is derived from the Greek word "bio" meaning "life" and the suffix "ology" meaning "study of.")

The scientific method was used in ancient times, but it was first documented by England's Sir Francis Bacon (1561–1626), who set up the first methodology for scientific inquiry. The scientific method is not exclusively used by biologists but can be applied to almost all fields of study as a logical, rational problem-solving method. Natural history observations and advances in microscopy have also had a profound impact on biological thinking. In the early 19th century, a number of biologists pointed to the central importance of the cell and in 1838, Schleiden and Schwann began promoting the now universal ideas of the cell theory. Jean-Baptiste Lamarck was the first to present a coherent theory of evolution, although it was the British naturalist Charles Darwin who spread the theory of natural selection throughout the scientific community. In 1953, the discovery of the double-helical structure of DNA marked the transition to the era of molecular genetics.

Video



Learn about Karl Popper and falsifiable hypotheses in this 11-minute video.
Question after watching: How does the idea of falsification change how you may have learned about science in the past?

Scientific Reasoning

One thing is common to all forms of science: an ultimate goal "to know." Curiosity and inquiry are the driving forces for the development of science. Scientists seek to understand the world and the way it operates. To do this, they use two methods of logical thinking: inductive reasoning and deductive reasoning (Figure 0.2.2).

Inductive reasoning is a form of logical thinking that uses related observations to arrive at a general conclusion. This type of reasoning is common in descriptive science. A life scientist such as a biologist makes observations and records them. These data can be qualitative or quantitative, and the raw data can be supplemented with drawings, pictures, photos, or videos. From many observations, the scientist can infer conclusions (inductions) based on evidence. Inductive reasoning involves formulating generalizations inferred from careful observation and the analysis of a large amount of data. Brain studies provide an example. In this type of research, many live brains are observed while people are doing a specific activity, such as viewing images of food. The part of the brain that "lights up" during this activity is then predicted to be the part controlling the response to the selected stimulus, in this case, images of food. Then, researchers can stimulate that part of the brain to see if similar responses result.

Deductive reasoning or deduction is the type of logic used in hypothesis-based science. In deductive reason, the pattern of thinking moves in the opposite direction as compared to inductive reasoning. Deductive reasoning is a form of logical thinking that uses a general principle or law to forecast specific results. From those general principles, a scientist can extrapolate and predict the specific results that would be valid as long as the general principles are valid. Studies in climate change can illustrate this type of reasoning. For example, scientists may predict that if the climate becomes warmer in a particular region, then the distribution of plants and animals should change. These predictions have been made and tested, and many such changes have been found, such as the modification of arable areas for agriculture, with change based on temperature averages.

Two Types of Reasoning

Inductive reasoning: from a number of observations, a general conclusion is drawn.	**Deductive reasoning:** from a general premise, specific results are predicted.
Observations • Members of a species are not all the same. • Individuals compete for resources. • Species are generally adapted to their environment.	**General premise** Individuals most adapted to their environment are more likely to survive and pass their traits on to the next generation.
Conclusion Individuals most adapted to their environment are more likely to survive and pass their traits to the next generation.	**Predicted results** If the average temperature in an ecosystem increases due to climate change, individuals better adapted to warmer temperatures will outcompete those that are not.

Figure 0.2.2: Inductive vs Deductive Reasoning

? Optional Activity 0.2.1

Decide if each of the following is an example of inductive or deductive reasoning.

1. All flying birds and insects have wings. Birds and insects flap their wings as they move through the air. Therefore, wings enable flight.
2. Insects generally survive mild winters better than harsh ones. Therefore, insect pests will become more problematic if global temperatures increase.
3. Chromosomes, the carriers of DNA, separate into daughter cells during cell division. Therefore, DNA is the genetic material.

4. Animals as diverse as humans, insects, and wolves all exhibit social behavior. Therefore, social behavior must have an evolutionary advantage.

Answer

1: inductive; 2: deductive; 3: deductive; 4: inductive.

Video





Many students confuse deductive reasoning with inductive reasoning, and vice versa. Learn the difference in this 3-minute video.
Question after watching: Reflect on incidents/events in your life where you applied deductive and inductive reasoning. Describe them and why they are instances of inductive and deductive reasoning.

Both types of logical thinking are related to the two main pathways of scientific study: **descriptive science** and **hypothesis-based science**. Descriptive (or discovery) science, which is usually inductive, aims to observe, explore, and discover. Hypothesis-based science, which is usually deductive, begins with a specific question or problem and a potential answer or solution that can be tested. In hypothesis-based science, specific results are predicted from a general premise.

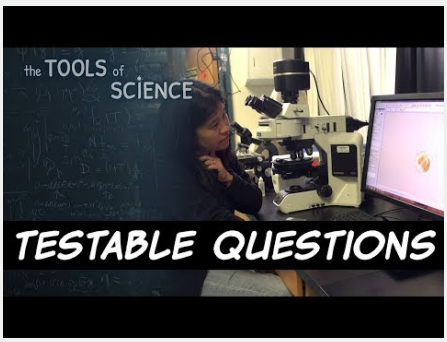
The boundary between descriptive science and hypothesis-based science is often blurred, and most scientific endeavors combine both approaches. Inductive and deductive reasoning are often used in tandem to advance scientific knowledge. The fuzzy boundary becomes apparent when thinking about how easily observation can lead to specific questions. For example, a gentleman in the 1940s observed that the burr seeds that stuck to his clothes and his dog's fur had a tiny hook structure. On closer inspection, he discovered that the burrs' gripping device was more reliable than a zipper. He eventually developed a company and produced the hook-and-loop fastener popularly known today as Velcro. Descriptive science and hypothesis-based science are in continuous dialogue.

The Scientific Method

Biologists study the living world by posing questions about it and seeking science-based responses. This approach is common to other sciences as well and is often referred to as the scientific method. The scientific process typically starts with an observation (often a problem to be solved) that leads to a question. Let's think about a simple problem that starts with an observation and apply the scientific method to solve the problem. One Monday morning, a student arrives at class and quickly discovers that the classroom is too warm. That is an observation that also describes a problem: the classroom is too warm. The student then asks a question: "Why is the classroom so warm?"

Video





Learn about the 5 criteria that a testable question should meet in this 7.5-minute video.

? Optional Activity 0.2.2

Read the following questions. Does the statement lend itself to investigation using the scientific method? In other words, is the hypothesis falsifiable (can be proven false)?

1. Is macaroni and cheese tastier than broccoli soup?
2. Are hummingbirds attracted to the color red?
3. Is the moon made out of green cheese?
4. Is plagiarism dishonest?

a. Questions 1 and 2 are subjective and cannot be disproven using scientific method. Questions 3 and 4 can be tested using scientific method.

b. Questions 3 and 4 are subjective and cannot be disproven using scientific method. Questions 1 and 2 can be tested using scientific method.

c. Questions 1 and 3 are subjective and cannot be disproven using scientific method. Questions 2 and 4 can be tested using scientific method.

d. Questions 1 and 4 are subjective and cannot be disproven using scientific method. Questions 2 and 3 can be tested using scientific method.

Answer

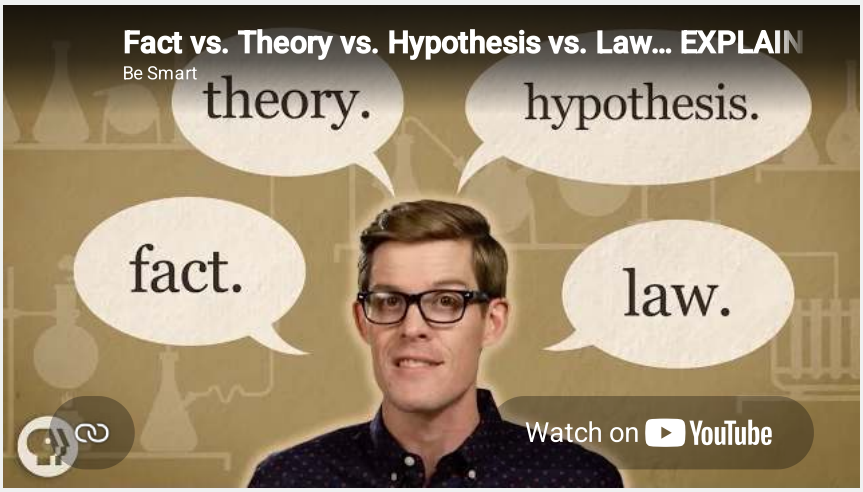
d. Questions 1 and 4 are subjective and cannot be disproven using scientific method. Questions 2 and 3 can be tested using scientific method.

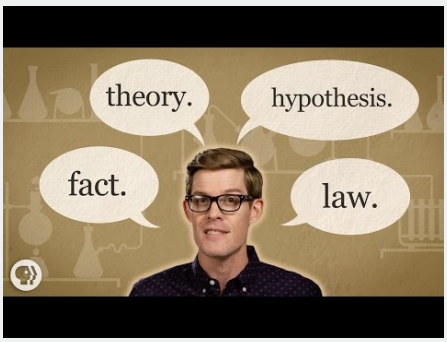
Proposing a Hypothesis

Recall that a hypothesis is a suggested explanation that can be tested. To solve a problem, several hypotheses may be proposed. For example, one hypothesis might be, “The classroom is warm because no one turned on the air conditioning.” But there could be other responses to the question, and therefore other hypotheses may be proposed. A second hypothesis might be, “The classroom is warm because there is a power failure, and so the air conditioning doesn’t work.”

Once a hypothesis has been selected, the student can make a **prediction**. A prediction is similar to a hypothesis but it typically has the format “If . . . then . . . .” For example, the prediction for the first hypothesis might be, “*If* the student turns on the air conditioning, *then* the classroom will no longer be too warm.”

Video





In this 7-minute video, learn the difference between a fact, a theory, a hypothesis, and a scientific law.
Question BEFORE and AFTER watching: How would you define hypothesis and theory?

Testing a Hypothesis

A valid hypothesis must be testable. It should also be **falsifiable**, meaning that it can be disproven by experimental results. Importantly, science does not claim to "prove" anything because scientific understandings are always subject to modification with further information. This step—openness to disproving ideas—is what distinguishes sciences from non-sciences. The presence of the supernatural, for instance, is neither testable nor falsifiable. To test a hypothesis, a researcher will conduct one or more experiments designed to eliminate one or more of the hypotheses. Each experiment will have one or more variables and one or more controls. A **variable** is any part of the experiment that can vary or change during the experiment. The **control group** contains all of the same conditions experimental group EXCEPT for the variable being tested. Therefore, if the results of the **experimental group** differ from the control group, the difference must be due to the manipulation, rather than some outside factor. Identify the variables and controls in the examples from the section above.

Revisit the hypotheses from the section above:

1. The classroom is warm because no one turned on the air conditioning.
2. The classroom is warm because there is a power failure, and so the air conditioning doesn't work.

To test the first hypothesis, the student would find out if the air conditioning is on. If the air conditioning is turned on but does not work, there should be another reason, and this hypothesis should be rejected. To test the second hypothesis, the student could check if the lights in the classroom are functional. If so, there is no power failure and this hypothesis should be rejected. Each hypothesis should be tested by carrying out appropriate experiments. Be aware that rejecting one hypothesis does not determine whether or not the other hypotheses can be accepted; it simply eliminates one hypothesis that is not valid (Figure 0.2.4). Using the scientific method, the hypotheses that are inconsistent with experimental data are rejected.

While this "warm classroom" example is based on observational results, other hypotheses and experiments might have clearer controls. For instance, a student might attend class on Monday and realize she had difficulty concentrating on the lecture. One observation to explain this occurrence might be, "When I eat breakfast before class, I am better able to pay attention." The student could then design an experiment with a control to test this hypothesis, including keeping all details of their morning the same but eating breakfast one day versus another to see how their attention holds in class.

The scientific method may seem too rigid and structured (Figure 0.2.3). It is important to keep in mind that, although scientists often follow this sequence, there is flexibility. In fact, the scientific process is much more complex in practice. Sometimes an experiment leads to conclusions that favor a change in approach; often, an experiment brings entirely new scientific questions to the puzzle. Many times, science does not operate in a linear fashion; instead, scientists continually draw inferences and make generalizations, finding patterns as their research proceeds. Scientific reasoning is more complex than the scientific method alone suggests. Notice, too, that the scientific method can be applied to solving problems that aren't necessarily scientific in nature.

Video





In this 5-minute video, explore how scientists designed and implemented a sampling and data collection plan to answer scientific questions. Questions after watching: What are important things to consider when selecting samples?

Video





In this 6-minute video, explore why data is critically important to the scientific process, what makes good data, and how to use data correctly. Question after watching: What is the distinction and/or relationship between variables and data?

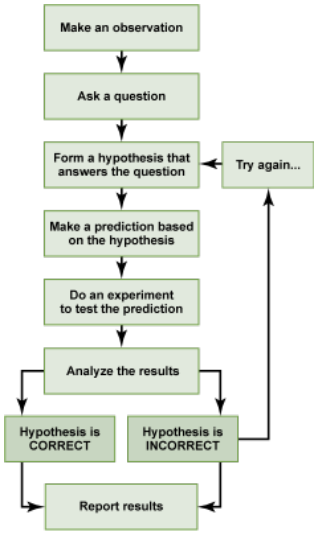


Figure 0.2.3: The traditional view of the scientific method.

? Optional Activity 0.2.3

In the example below, the scientific method is used to solve an everyday problem. Order the scientific method steps (numbered items) with the process of solving the everyday problem (lettered items). Based on the results of the experiment, is the hypothesis correct? If it is incorrect, propose some alternative hypotheses.

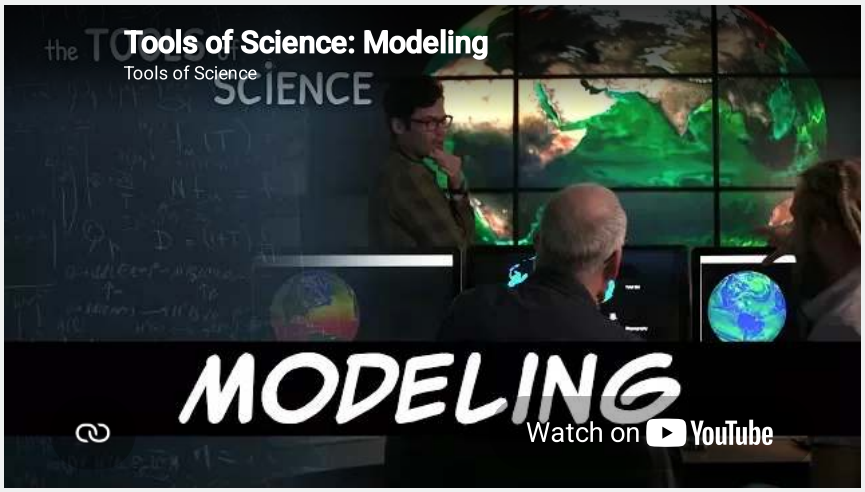
1. Observation
2. Question
3. Hypothesis (answer)
4. Prediction
5. Experiment
6. Result

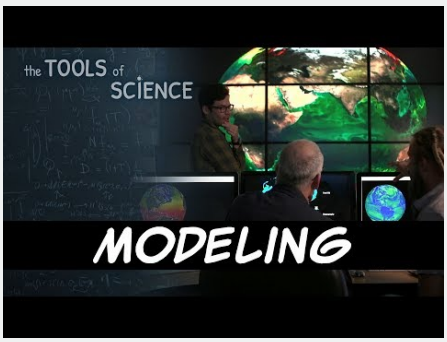
A. There is something wrong with the electrical outlet.
B. If something is wrong with the outlet, my coffeemaker also won't work when plugged into it.
C. My toaster doesn't toast my bread.
D. I plug my coffee maker into the outlet.
E. My coffeemaker works.
F. Why doesn't my toaster work?

Answer

1: C; 2: F; 3: A; 4: B; 5: D; 6: E. The original hypothesis is incorrect, as the coffeemaker works when plugged into the outlet. Alternative hypotheses include that the toaster might be broken or that the toaster wasn't turned on.

Video





In this 6-minute video, the critical importance of mathematical models to the scientific process is explored.
Question: Why is modeling such a fundamentally important tool?

Video





Discover why collaboration among scientists with different backgrounds and expertise is essential for strong science investigations in this 6.5-minute video.
Question after watching: The research expedition includes several research teams. Why is that?

Video





See how science REALLY works in this 5-minute video.
Question after watching: Why do they use the pinball game analogy for describing how science works?

Optional Resource

Find a more realistic, but more complex, diagram of the scientific method from the University of California - Berkeley here: https://undsci.berkeley.edu/lessons/pdfs/complex_flow_handout.pdf

Pseudoscience

Pseudoscience is a claim, belief, or practice that is presented as scientific but does not adhere to the standards and methods of science. True science is based on repeated evidence-gathering and testing of falsifiable hypotheses. Pseudoscience does not adhere to these criteria. Pseudoscience is often known as fringe or alternative science. It usually lacks the carefully-controlled and thoughtfully-interpreted experiments which provide the foundation of the natural sciences and which contribute to their advancement. In addition to phrenology, some other examples of pseudoscience include astrology, extrasensory perception (ESP), reflexology, reincarnation, and Scientology

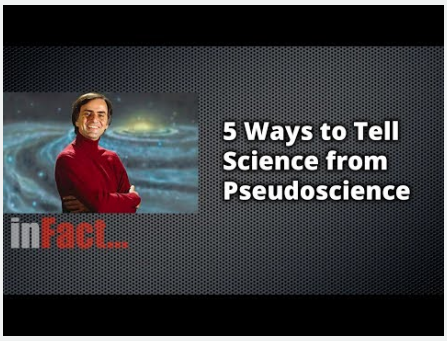
Characteristics of Pseudoscience

Whether a field is actually science or just pseudoscience is not always clear. However, pseudoscience generally exhibits certain common characteristics. Indicators of pseudoscience include:

- *The use of vague, exaggerated, or untestable claims:* Many claims made by pseudoscience cannot be tested with evidence. As a result, they cannot be falsified, even if they are not true.
- *An over-reliance on confirmation rather than refutation:* Any incident that appears to justify a pseudoscience claim is treated as proof of the claim. Claims are assumed true until proven otherwise, and the burden of disproof is placed on skeptics of the claim.
- *A lack of openness to testing by other experts:* Practitioners of pseudoscience avoid subjecting their ideas to peer review. They may refuse to share their data and justify the need for secrecy with claims of proprietary or privacy.
- *An absence of progress in advancing knowledge:* In pseudoscience, ideas are not subjected to repeated testing followed by rejection or refinement, as hypotheses are in true science. Ideas in pseudoscience may remain unchanged for hundreds — or even thousands — of years. In fact, the older an idea is, the more it tends to be trusted in pseudoscience.
- *Personalization of issues:* Proponents of pseudoscience adopt beliefs that have little or no rational basis, so they may try to confirm their beliefs by treating critics as enemies. Instead of arguing to support their own beliefs, they attack the motives and character of their critics.
- *The use of misleading language:* Followers of pseudoscience may use scientific-sounding terms to make their ideas sound more convincing. For example, they may use the formal name dihydrogen monoxide to refer to plain old water.

Video





This 3.5-minute video reviews what is considered pseudoscience.
Question after watching: What are some instances of pseudoscience that you have seen or heard recently?

Persistence of Pseudoscience

Despite failing to meet scientific standards, many pseudosciences survive. Some pseudosciences remain very popular with large numbers of believers. A good example is astrology.

Astrology claims to study the movements and relative positions of celestial objects as a means for divining information about human affairs and terrestrial events. Many ancient cultures attached importance to astronomical events, and some developed elaborate systems for predicting terrestrial events from celestial observations. Throughout most of its history in the West, astrology was actually considered a scholarly tradition and was common in academic circles. With the advent of modern Western sciences and the process of scientific inquiry, however, astrology was called into question. It was challenged on both theoretical and experimental grounds. Eventually, astrology was shown to have no scientific validity or explanatory power.

Today, astrology is considered a pseudoscience, yet it continues to have many devotees. Many people know their astrological sign, and some are familiar with the supposed personality traits associated with their "sign". Astrological readings and horoscopes are readily available online and in print media, and a lot of people read them, even if only occasionally. Some believe that astrology is scientific. Studies suggest that the persistent popularity of pseudosciences such as astrology is due to

misunderstandings of scientific principles and methodology. Alternatively, some are not convinced by scientific arguments that go against their personal beliefs and this, in the end, can do real harm to themselves or others.

Dangers of Pseudoscience

Belief in astrology is unlikely to cause a person harm, but belief in some other pseudosciences might — especially in healthcare-related areas. Treatments that seem scientific but are not may be ineffective, expensive, and even dangerous to patients. Seeking out pseudoscientific treatments may also delay or preclude patients from seeking scientifically-based medical treatments that have been tested and found safe and effective. In short, following pseudoscience instead of established health care practices may be harmful.

Scientific Hoaxes, Frauds, and Fallacies

Pseudoscience is not the only way that science may be misused. Scientific **hoaxes,** frauds, and fallacies may misdirect the pursuit of science, put patients at risk, or mislead and confuse the public. An example of each of these misuses of science and its negative effects is described below.

The Vaccine-Autism Fraud

While it is not true, you may have heard that certain vaccines put the health of young children at risk. This persistent idea is not supported by scientific evidence or accepted by the vast majority of experts in the field. It stems largely from an elaborate medical research fraud that was reported in a 1998 article published in the respected British medical journal, *The Lancet*. The main author of the article was a British physician named Andrew Wakefield. In the article, Wakefield and his colleagues described case histories of only 12 children, most of whom were reported to have developed autism soon after the administration of the MMR (measles, mumps, rubella) vaccine.

There were a whole host of problems with this study, including falsification of research, ethics violations, and experimental design problems. The paper has been retracted (a very big deal in the science community), most of the co-authors have retracted their authorship, and Wakefield lost his medical license. It also later emerged that Wakefield had received research funding from a group of people who were suing vaccine manufacturers. Thousands of follow-up studies have failed to show any association between the MMR vaccine and autism. Unfortunately, by then, the damage had already been done. Parents afraid that their children would develop autism had refrained from having them vaccinated. British MMR vaccination rates fell from nearly 100 percent to 80 percent in the years following the study. The consensus of medical experts today is that Wakefield's fraud put hundreds of thousands of children at risk because of the lower vaccination rates and also diverted research efforts and funding away from finding the true cause of autism.

Correlation-Causation Fallacy

Many statistical tests used in scientific research calculate correlations between variables. **Correlation** refers to how closely related two data sets are, which may be a useful starting point for further investigation. Correlation, however, is also one of the most misused types of evidence, primarily because of the logical fallacy that correlation implies causation. In reality, just because two variables are correlated does not *necessarily* mean that either variable causes the other.

A few simple examples, illustrated by the graphs below, can be used to demonstrate the correlation-causation fallacy. Assume a study found that both per capita consumption of mozzarella cheese and the number of Civil Engineering doctorates awarded are correlated; that is, rates of both events increase together Figure 0.2.4. If correlation really did imply causation, then you could conclude from the second example that the increase in age of Miss America causes an increase in murders of a specific type or vice versa Figure 0.2.5.

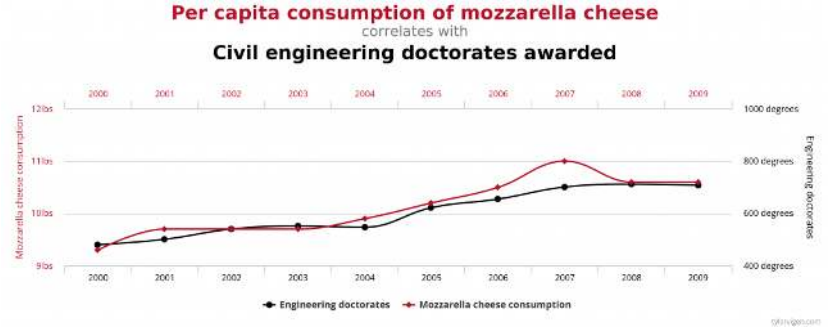


Figure 0.2.4 Spurious Correlations [Causation Fallacy] – Consumption of mozzarella cheese and awarded Doctorates

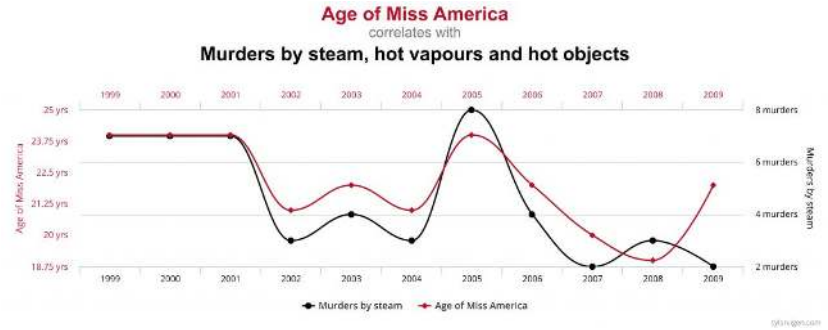


Figure 0.2.5: Spurious Correlations (Causation Fallacy)- Miss America and Murder

Video





Watch this 4-minute video to learn how to spot a misleading graph.
Question after watching: How can graphs present an opinion?

HRT and CHD

An actual example of the correlation-causation fallacy occurred during the latter half of the 20th century. Numerous studies showed that women taking hormone replacement therapy (HRT) to treat menopausal symptoms also had a lower-than-average incidence of coronary heart disease (CHD). This correlation was misinterpreted as evidence that HRT protects women against CHD. Subsequent studies that controlled other factors related to CHD disproved this presumed causal connection. The studies found that women taking HRT were more likely to come from higher socio-economic groups, with better-than-average diets and exercise regimens. Rather than HRT causing lower CHD incidence, these studies concluded that HRT and lower CHD were both effects of higher socio-economic status and related lifestyle factors.

Video





How statistics can be misleading
Question after watching:
What types of motivation could be at play when people or organizations present statistics?

Finally, read through this "Rough Guide to Spotting Bad Science" infographic from Compound Interest:

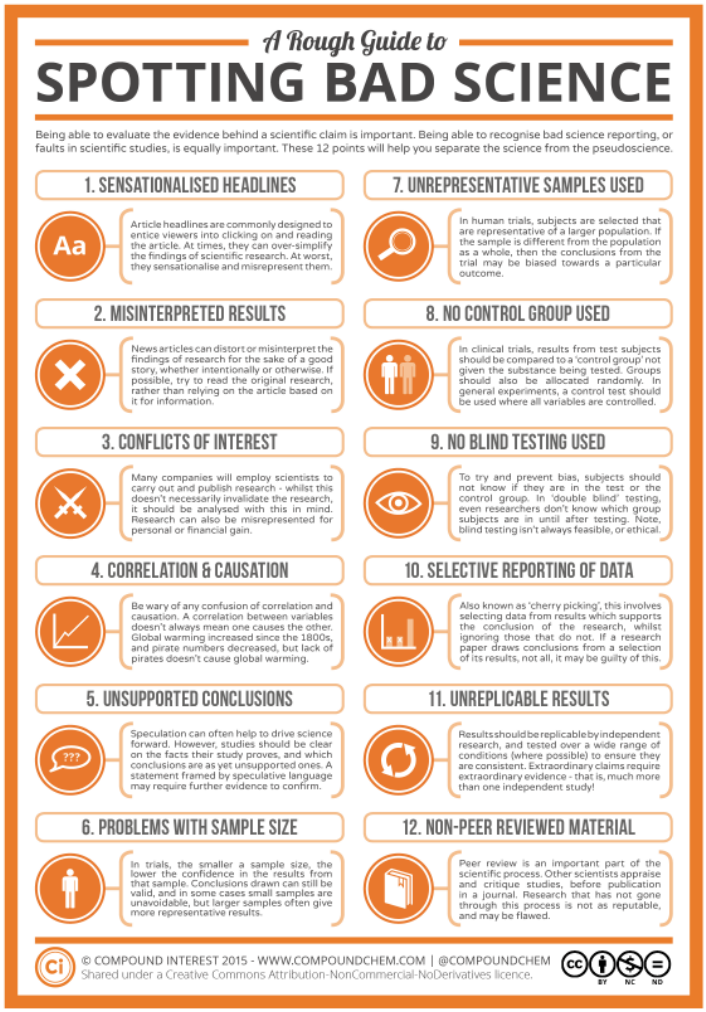


Figure 0.2.6: A Rough Guide to Spotting Bad Science.

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0.3: The Role of Science in Society

The Role of Science in Society

- Please read and watch the following Mandatory Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 1.5 hours.
- To navigate, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Appreciate the importance of science in culture and society;
- Compare and contrast basic and applied science;
- Explain how scientists disseminate their work;
- Describe characteristics of Indigenous ways of knowing about the natural world;
- Identify how the process of science and Indigenous ways of knowing may complement one another.

Science and Culture

From the United Nations Educational, Scientific and Cultural Organization (UNESCO):

> *"Science is the greatest collective endeavor. It contributes to ensuring a longer and healthier life, monitors our health, provides medicine to cure our diseases, alleviates aches and pains, helps us to provide water for our basic needs – including our food, provides energy and makes life more fun, including sports, music, entertainment and the latest communication technology. Last but not least, it nourishes our spirit.*
>
> *Science generates solutions for everyday life and helps us to answer the great mysteries of the universe. In other words, science is one of the most important channels of knowledge. It has a specific role, as well as a variety of functions for the benefit of our society: creating new knowledge, improving education, and increasing the quality of our lives.*
>
> *Science must respond to societal needs and global challenges. Public understanding and engagement with science, and citizen participation including through the popularization of science are essential to equip citizens to make informed personal and professional choices. Governments need to make decisions based on quality scientific information on issues such as health and agriculture, and parliaments need to legislate on societal issues which necessitate the latest scientific knowledge. National governments need to understand the science behind major global challenges such as climate change, ocean health, biodiversity loss and freshwater security.*
>
> *To face sustainable development challenges, governments and citizens alike must understand the language of science and must become scientifically literate. On the other hand, scientists must understand the problems policy-makers face and endeavor to make the results of their research relevant and comprehensible to society.*
>
> *Challenges today cut across the traditional boundaries of disciplines and stretch across the lifecycle of innovation -- from research to knowledge development and its application. Science, technology and innovation must drive our pursuit of more equitable and sustainable development"* (2021).

Two Types of Science: Basic Science and Applied Science

The scientific community has been debating for the last few decades about the value of different types of science. Is it valuable to pursue science for the sake of simply gaining knowledge, or does scientific knowledge only have worth if we can apply it to solving a specific problem or to bettering our lives? This question focuses on the differences between two types of science: **basic science** and **applied science**.

Basic science or “pure” science seeks to expand knowledge regardless of the short-term application of that knowledge. It is not focused on developing a product or a service of immediate public or commercial value. The immediate goal of basic science is

knowledge for knowledge's sake, though this does not mean that, in the end, it may not result in a practical application.

In contrast, applied science or "technology," aims to use science to solve real-world problems, making it possible, for example, to improve a crop yield, find a cure for a particular disease, or save animals threatened by a natural disaster (Figure 0.3.1). In applied science, the problem is usually defined for the researcher.



Figure 0.3.1: After Hurricane Ike struck the Gulf Coast in 2008, the U.S. Fish and Wildlife Service rescued this brown pelican. Thanks to applied science, scientists knew how to rehabilitate the bird. (credit: FEMA)

Some individuals may perceive applied science as "useful" and basic science as "useless." A question these people might pose to a scientist advocating knowledge acquisition would be, "What for?" A careful look at the history of science, however, reveals that basic knowledge has resulted in many remarkable applications of great value. Many scientists think that a basic understanding of science is necessary before an application is developed; therefore, applied science relies on the results generated through basic science. Other scientists think that it is time to move on from basic science and instead to find solutions to actual problems. Both approaches are valid. It is true that there are problems that demand immediate attention; however, few solutions would be found without the help of the wide knowledge foundation generated through basic science.

One example of how basic and applied science can work together to solve practical problems occurred after the discovery of DNA structure led to an understanding of the molecular mechanisms governing DNA replication. Strands of DNA, unique in every human, are found in our cells, where they provide the instructions necessary for life. During DNA replication, DNA makes new copies of itself, shortly before a cell divides. Understanding the mechanisms of DNA replication enabled scientists to develop laboratory techniques that are now used to identify genetic diseases, pinpoint individuals who were at a crime scene, and determine paternity. Without basic science, it is unlikely that applied science would exist.

Another example of the link between basic and applied research is the Human Genome Project, a study in which each human chromosome was analyzed and mapped to determine the precise sequence of DNA subunits and the exact location of each gene. (The gene is the basic unit of heredity; an individual's complete collection of genes is his or her genome). Other less complex organisms have also been studied as part of this project in order to gain a better understanding of human chromosomes. The Human Genome Project relied on basic research carried out with simple organisms and, later, with the human genome (Figure 0.3.2). An important end goal eventually became using the data for applied research, seeking cures and early diagnoses for genetically related diseases.

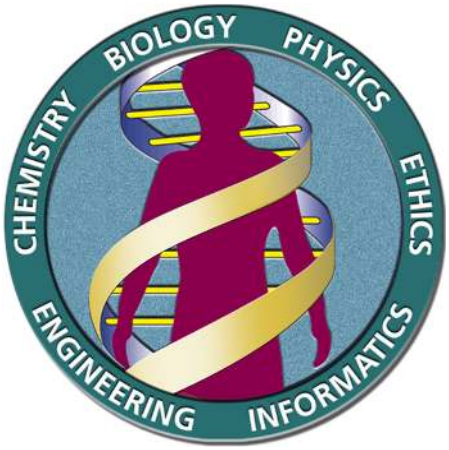


Figure 0.3.2: The Human Genome Project was a 13-year collaborative effort among researchers working in several different fields of science. The project, which sequenced the entire human genome, was completed in 2003. (credit: the U.S. Department of Energy Genome Programs (http://genomics.energy.gov))

While research efforts in both basic science and applied science are usually carefully planned, it is important to note that some discoveries are made by **serendipity**, that is, by means of a fortunate accident or a lucky surprise. Penicillin was discovered when biologist Alexander Fleming accidentally left a petri dish of *Staphylococcus* bacteria open. An unwanted mold grew on the dish, killing the bacteria. The mold turned out to be *Penicillium*, and a new antibiotic was discovered. Even in the highly organized world of science, luck—when combined with an observant, curious mind—can lead to unexpected breakthroughs.

Video





Watch this video to see how science is playing a role in understanding Peary caribou in Canada.
Question after watching:
What type of research is this? Basic or applied?

Reporting Scientific Work

Whether scientific research is basic science or applied science, scientists must share their findings in order for other researchers to expand and build upon their discoveries. Collaboration with other scientists—when planning, conducting, and analyzing results—are all important for scientific research. For this reason, important aspects of a scientist's work are communicating with peers and disseminating results to peers. Scientists can share results by presenting them at a scientific meeting or conference, but this approach can reach only the select few who are present. Instead, most scientists present their results in peer-reviewed manuscripts that are published in scientific journals. Peer-reviewed manuscripts are scientific papers that are reviewed by a scientist's colleagues, or peers. These colleagues are qualified individuals, often experts in the same research area, who judge whether or not the scientist's work is suitable for publication. The process of **peer review** helps to ensure that the research described in a scientific paper or grant proposal is original, significant, logical, and thorough. Grant proposals, which are requests for research funding, are also subject to peer review. Scientists publish their work so other scientists can reproduce their experiments under similar or different conditions to expand on the findings. The experimental results must be consistent with the findings of other scientists.

A scientific paper is very different from creative writing. Although creativity is required to design experiments, there are fixed guidelines when it comes to presenting scientific results. First, scientific writing should be concise and accurate. A scientific paper needs to be succinct but detailed enough to allow peers to reproduce the experiments.

The scientific paper consists of several specific sections—introduction, materials and methods, results, and discussion. This structure is sometimes called the "**IMRaD**" format. There are usually acknowledgment and reference sections as well as an abstract (a concise summary) at the beginning of the paper. There might be additional sections depending on the type of paper and the journal where it will be published; for example, some review papers require an outline.

The **introduction** starts with brief, but broad, background information about what is known in the field. A good introduction also gives the rationale of the work; it justifies the work carried out and is where the hypothesis or research question driving the research will be presented. The introduction may also briefly mention the results of the paper. The introduction refers to the published scientific work of others and therefore requires citations following the style of the journal. Using the work or ideas of others without proper citation is considered plagiarism.

The **materials and methods** section includes a complete and accurate description of the substances used, and the method and techniques used by the researchers to gather data. The description should be thorough enough to allow another researcher to repeat the experiment and obtain similar results, but it does not have to be verbose. This section will also include information on how measurements were made and what types of calculations and statistical analyses were used to examine raw data. Although the materials and methods section gives an accurate description of the experiments, it does not discuss them.

Some journals require a **results** section followed by a **discussion** section, but some may combine both. If the journal does not allow the combination of both sections, the results section simply narrates the findings without any further interpretation. The results are

presented by means of tables or graphs, but no duplicate information should be presented. In the discussion section, the researcher will interpret the results, describe how variables may be related, and attempt to explain the observations. It is indispensable to conduct an extensive literature search to put the results in the context of previously published scientific research. Therefore, proper **citations** are included in this section as well.

Finally, a **conclusion** section may be used to summarize the importance of the experimental findings. Most often, the conclusions are included in the discussion. While the scientific paper almost certainly answered one or more scientific questions that were stated, any good research should lead to more questions. Therefore, a well-done scientific paper leaves doors open for the researcher and others to continue and expand on the findings.

Review articles do not follow the IMRAD format because they do not present original scientific findings, or primary literature; instead, they summarize and comment on findings that were published as primary literature and typically include extensive reference sections. They follow specific methods of searching and summarizing the scientific literature, to ensure that their findings are reproducible.

Indigenous Science

The following text may be different than text that you have come across before in a science context because Indigenous Science will be woven throughout the content. You will find this content as green call-out boxes throughout this text.

Now that you have read this unit, the following piece has been included to provide you with another perspective on science and culture. Consider this not as an alternative to what you have already learned but an examination of how each can contribute to a better understanding of nature, the world, and its importance. Indigenous Science, explained below, is formally known to many biologists and ecologists as Traditional Ecological Knowledge (TEK); this text will use TEK throughout the rest of the Units.

Indigenous Connections

It is important to balance and consider Indigenous Science, that which recognizes the knowledge inherent in each culture: "every culture and every society has its own science, and its function is sustaining its mother society and culture" (Yamada, 1970, p. 585). Cultural diversity suggests that Western Science (WS) and Indigenous Science (IS) should be viewed as co-existing or parallel. Hatcher, Marshall, and Marshall (2009, p. 15) describe Indigenous Science metaphorically as a "living knowledge" that requires less dependence on knowledge transfer from books and requires "knowledge gardening with living knowledge keepers," which differs from Western Science. As you study biology, it is important to balance and consider the traditional contexts of Indigenous Science (IS) with Western Science (WS) evidence and reason.

The traditional wisdom component of IS—the values and ways of decision-making relating to science knowledge—is particularly rich in time-tested approaches that foster sustainability and environmental integrity. Western Science (WS) is the most dominant science in the world today and is widely thought of as 'officially sanctioned science'. However, because WS has been implicated in many of the world's ecological disasters—pesticide contamination, introduced species, dams and water diversions that have impacted salmon and other indigenous species—it seems that reliance on Western Science alone can be seen as increasingly problematic and even counterproductive.

The process of generating or learning Indigenous ways of living in nature is *coming to know* (Cajete, 2000; Peat, 1994), a phrase that connotes a journey. *Coming to know* differs from a Eurocentric science process *to know* or *to discover* that connotes a destination, such as a patent or published record of discovery. Indigenous *coming to know* is a journey toward wisdom or a journey of wisdom in action, not a discovery of knowledge (Aikenhead & Ogawa, 2007). For Michell (2005), *coming to know* includes the goal of living in harmony with nature for the survival of the community. "Nature provides a blueprint of how to live well and all that is necessary to sustain life" (Michell, 2005, p. 39).

TEK combines current observation with wisdom, knowledge, and experience that has been acquired over thousands of years of direct human contact with specific environments. TEK interprets how the world works from the cultural perspective unique to a particular group of Indigenous peoples. Although the term TEK came into widespread use in the 1980's, TEK itself is timeless and predates written record (Corsiglia & Snively, 1997). The stories and testimonies of Indigenous peoples are usually related to a home place or territory. TEK embodies both remembered sensory information built upon repeated observation, and formal understandings that are usually transmitted orally in story form or ceremonial form with abstract principles and

important information encapsulated in metaphor (Cruikshank, 1991; Turner, Ignace, & Ignace, 2000). Perhaps the most useful way to think about Indigenous Science is that it is complementary to Western Science and not a replacement for it. Rooted in different worldviews, Indigenous and Western Science are not easy to combine, and it may not be desirable to meld the two. Each knowledge system is legitimate in its own right. The two kinds of knowledge may be pursued separately but in parallel, enriching one another as needed (Berkes, 2012). As such, *weaving TEK* with western science throughout this text will help you develop a deeper understanding of key biology concepts from multiple perspectives.

Numerous traditional peoples' scientific and technological contributions have been incorporated in modern applied sciences such as ecology, biology, medicine, architecture, engineering, geology, pharmacology, agriculture, horticulture, agronomy, metallurgy, navigation, astronomy, animal husbandry, fish and wildlife management, nautical science, plant breeding, and military and political science (Berkes, 2012; Turner & Peacock, 2005; Deur & Turner, 2005; Turner, 2014a, 2014b; Weatherford, 1988, 1991). The truth is, directly or indirectly, we are all benefiting from Indigenous scientific and technological innovations every time we dine, clothe ourselves, travel or go to the doctor.

TEK provides invaluable time-tested resource management practices that can be used alongside WS to develop more workable and effective approaches to current resource management strategies than either could accomplish alone. In fact, it has become a policy requirement in Canada, and in particular Northern Canada, that TEK be incorporated into environmental assessments affecting wildlife management including: migratory birds, species at risk, forest practices, and fisheries management (Usher, 2000).

Some of the contributions of TEK and Indigenous Science scholarship to contemporary environmental knowledge, conservation and resource management worldwide (acknowledged by Western scientists) are outlined below:

- Perceptive investigations of traditional environmental knowledge systems provide important biological and ecological insights (Berkes 2012; Houde, 2007; Turner & Peacock, 2005; Turner, 2014a, 2014b; Usher, 2000; Warren, 1997).
- Help locate rare and endangered species and provide cost-effective shortcuts for investigating the local resource bases. Local knowledge makes it possible to survey and map in a few days what would otherwise take months, for example, soil types, plant and animal species, migration pathways, and aggregation sites (Berkes, 2012; Usher, 2000; Warren, 1997).
- Provide knowledge of time-tested resource management practices and can be used to develop workable approaches to current resource management strategies (Houde, 2007; Turner & Peacock, 2005; Usher, 2000; Warren, et. al., 1993).
- Provides time-tested in-depth knowledge of the local area (past and present) that can be triangulated with WS resulting in more accurate environmental assessment and impact statements. People who depend on local resources for their livelihood are often able to assess the true costs and benefits of development better than any evaluator from outside (Houde, 2007; Warren, et. al, 1993; 1997).
- Provides experience-based value statements about appropriate and ethical behavior with respect to animals and the environment (Berkes, 2012; Deur & Turner, 2005; Turner, 2014a, 2014b; Houde, 2007; Usher, 2000).

A key point here is that scientists may be unable to understand the complexity of ecosystems, especially northern or distant ecosystems, through sporadic observations, as opposed to lived experience.

Recognition of the importance of incorporating IS and TEK in environmental planning is explicitly addressed in reports and agreements in Canada and internationally. The Brundtland Commission report, *Our Common Future* (WCED: World Commission on Environment and Development, 1987), recognized the role of TEK in sustainable development; and the *Convention on Biological Diversity, Agenda 21* (UN Conference on the Environment, 1993), declared that Indigenous people possess important traditional scientific knowledge. The document *Science for the Twenty-first Century: A new Commitment* (UNESCO: United Nations Educational, Scientific and Cultural Organization, 2000), set new standards for respecting, protecting and utilizing Indigenous Knowledge. Working scientists worldwide, associated with hundreds of institutes, are collaborating with Elders and knowledge holders to collect and document examples of TEK and IS knowledge; this includes institutes in the US, Canada, Middle and South America, Africa, Europe, Australia, New Zealand, India, Russia, China and Japan.

Adapted from: Knowing Home: Braiding Indigenous Science with Western Science, Book 1 by Gloria Snively and Wanosts'a7 Lorna Williams (CC-NC-SA)

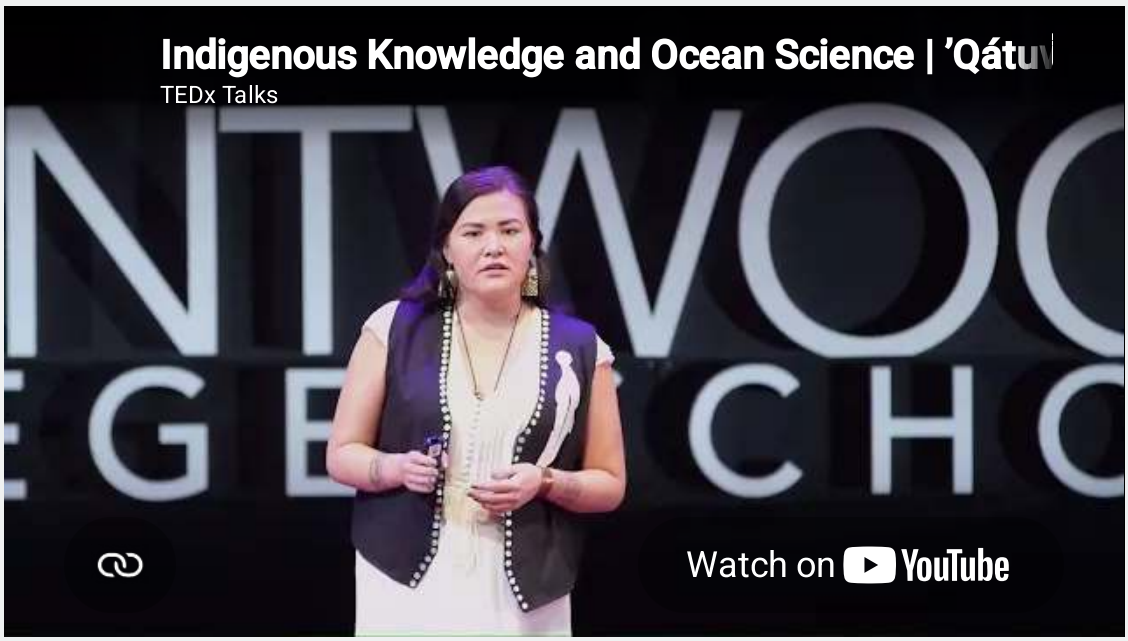
Videos


Modern Science, Native Knowledge
The Nature Conservancy
Watch on YouTube




How indigenous knowledge is changing what we k
Radio Canada International
Watch on YouTube







Watch the three videos above as examples of the TEK and WS working together.
Question after watching:
Do you know of other examples of TEK and IS from your province or region?

Indigenous Connection

Find an article entitled "First Nations communities bring expertise to Canada's scientific research" here from the Journal *Nature*: https://www.nature.com/articles/d41586-021-03060-x

References:

UNESCO. (2021). Science for Society. United Nations Education, Science, and Culture Organization. From: https://en.unesco.org/themes/science-society

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1.E: The Study of Life (Exercises)

1.1: The Science of Biology

Review Questions

The first forms of life on Earth were _____.

A. plants
B. microorganisms
C. birds
D. dinosaurs

Answer

B

A suggested and testable explanation for an event is called a _____.

A. hypothesis
B. variable
C. theory
D. control

Answer

A

Which of the following sciences is not considered a natural science?

A. biology
B. astronomy
C. physics
D. computer science

Answer

D

The type of logical thinking that uses related observations to arrive at a general conclusion is called _____.

A. deductive reasoning
B. the scientific method
C. hypothesis-based science
D. inductive reasoning

Answer

D

The process of _____ helps to ensure that a scientist's research is original, significant, logical, and thorough.

A. publication
B. public speaking
C. peer review
D. the scientific method

Answer

C

A person notices that her houseplants that are regularly exposed to music seem to grow more quickly than those in rooms with no music. As a result, she determines that plants grow better when exposed to music. This example most closely resembles which type of reasoning?

A. inductive reasoning
B. deductive reasoning
C. neither, because no hypothesis was made
D. both inductive and deductive reasoning

Answer

A

Free Response

Although the scientific method is used by most of the sciences, it can also be applied to everyday situations. Think about a problem that you may have at home, at school, or with your car, and apply the scientific method to solve it.

Answer

Answers will vary, but should apply the steps of the scientific method. One possibility could be a car which doesn't start. The hypothesis could be that the car doesn't start because the battery is dead. The experiment would be to change the battery or to charge the battery and then check whether the car starts or not. If it starts, the problem was due to the battery, and the hypothesis is accepted.

Give an example of how applied science has had a direct effect on your daily life.

Answer

Answers will vary. One example of how applied science has had a direct effect on daily life is the presence of vaccines. Vaccines to prevent diseases such polio, measles, tetanus, and even influenza affect daily life by contributing to individual and societal health.

Name two topics that are likely to be studied by biologists, and two areas of scientific study that would fall outside the realm of biology.

Answer

Answers will vary. Topics that fall inside the area of biological study include how diseases affect human bodies, how pollution impacts a species' habitat, and how plants respond to their environments. Topics that fall outside of biology (the "study of life") include how metamorphic rock is formed and how planetary orbits function.

Thinking about the topic of cancer, write a basic science question and an applied science question that a researcher interested in this topic might ask

Answer

Answers will vary. Basic science: What evolutionary purpose might cancer serve? Applied science: What strategies might be found to prevent cancer from reproducing at the cellular level?

1.2: Themes and Concepts of Biology

Review Questions

The smallest unit of biological structure that meets the functional requirements of “living” is the _____.

A. organ
B. organelle
C. cell
D. macromolecule

Answer

C

Viruses are not considered living because they _____.

A. are not made of cells
B. lack cell nuclei
C. do not contain DNA or RNA
D. cannot reproduce

Answer

A

The presence of a membrane-enclosed nucleus is a characteristic of _____.

A. prokaryotic cells
B. eukaryotic cells
C. living organisms
D. bacteria

Answer

B

A group of individuals of the same species living in the same area is called a(n) _____.

A. family
B. community
C. population
D. ecosystem

Answer

C

Which of the following sequences represents the hierarchy of biological organization from the most inclusive to the least complex level?

A. organelle, tissue, biosphere, ecosystem, population
B. organ, organism, tissue, organelle, molecule
C. organism, community, biosphere, molecule, tissue, organ
D. biosphere, ecosystem, community, population, organism

Answer

D

Where in a phylogenetic tree would you expect to find the organism that had evolved most recently?

A. at the base
B. within the branches
C. at the nodes
D. at the branch tips

Answer

D

Free Response

Select two items that biologists agree are necessary in order to consider an organism “alive.” For each, give an example of a non-living object that otherwise fits the definition of “alive.”

Answer

Answers will vary. Layers of sedimentary rock have order but are not alive. Technology is capable of regulation but is not, of itself, alive.

Consider the levels of organization of the biological world, and place each of these items in order from smallest level of organization to most encompassing: skin cell, elephant, water molecule, planet Earth, tropical rainforest, hydrogen atom, wolf pack, liver.

Answer

Smallest level of organization to largest: hydrogen atom, water molecule, skin cell, liver, elephant, wolf pack, tropical rainforest, planet Earth

You go for a long walk on a hot day. Give an example of a way in which homeostasis keeps your body healthy.

Answer

During your walk, you may begin to perspire, which cools your body and helps your body to maintain a constant internal temperature. You might also become thirsty and pause long enough for a cool drink, which will help to restore the water lost during perspiration.

Using examples, explain how biology can be studied from a microscopic approach to a global approach.

Answer

Researchers can approach biology from the smallest to the largest, and everything in between. For instance, an ecologist may study a population of individuals, the population’s community, the community’s ecosystem, and the ecosystem’s part in the biosphere. When studying an individual organism, a biologist could examine the cell and its organelles, the tissues that the cells make up, the organs and their respective organ systems, and the sum total—the organism itself.

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CHAPTER OVERVIEW

Chapter 1: Introduction to Ecology

Learning Objectives

- Use strategies of scientific inquiry to evaluate information, problems, and the validity of science.
- Perform simple analysis of data and use technology to draw conclusions about observed natural phenomena.
- Define ecology, ecosystem, community, and population.
- Compare and contrast ecology to the other biological, chemical, and physical sciences.

1.1: What is Ecology?
1.2: History of Ecology
1.3: Subdisciplines of Ecology
1.4: An Overview of Essential Mathematics Used in Science
1.5: Summarizing Data - Descriptive Statistics
1.6: Testing Hypotheses - Inferential Statistics

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1.1: What is Ecology?

Ecology is the study of the interactions of living organisms with their environment. One core goal of ecology is to understand the distribution and abundance of living things in the physical environment. Attainment of this goal requires the integration of scientific disciplines inside and outside of biology, such as biochemistry, physiology, evolution, biodiversity, molecular biology, geology, and climatology. Some ecological research also applies aspects of chemistry and physics, and it frequently uses mathematical models.

Video



Levels of Ecological Study

When a discipline such as biology is studied, it is often helpful to subdivide it into smaller, related areas. For instance, cell biologists interested in cell signaling need to understand the chemistry of the signal molecules (which are usually proteins) as well as the result of cell signaling. Ecologists interested in the factors that influence the survival of an endangered species might use mathematical models to predict how current conservation efforts affect endangered organisms. To produce a sound set of management options, a conservation biologist needs to collect accurate data, including current population size, factors affecting reproduction (like physiology and behavior), habitat requirements (such as plants and soils), and potential human influences on the endangered population and its habitat (which might be derived through studies in sociology and urban ecology). Within the discipline of ecology, researchers work at four specific levels, sometimes discretely and sometimes with overlap: organism, population, community, and ecosystem (Figure 1.1.1).

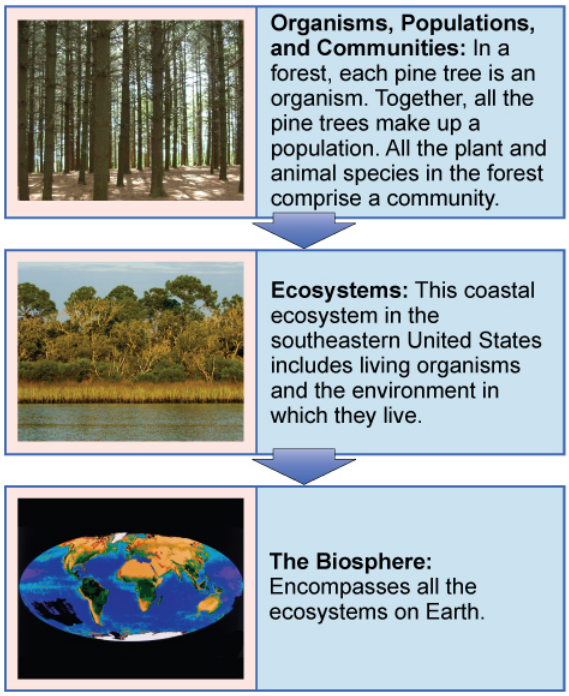


Figure 1.1.1: Ecologists study within several biological levels of organization. (credit “organisms”: modification of work by "Crystl"/Flickr; credit “ecosystems”: modification of work by Tom Carlisle, US Fish and Wildlife Service Headquarters; credit “biosphere”: NASA)

Organismal Ecology

Researchers studying ecology at the organismal level are interested in the adaptations that enable individuals to live in specific habitats. These adaptations can be morphological, physiological, and behavioral. For instance, the Karner blue butterfly *Lycaeides melissa samuelis* (Figure 1.1.2) is considered a specialist because the females preferentially oviposit (that is, lay eggs) on wild lupine. This preferential adaptation means that the Karner blue butterfly is highly dependent on the presence of wild lupine plants for its continued survival.



Figure 1.1.2: The Karner blue butterfly *Lycaeides melissa samuelis* is a rare butterfly that lives only in open areas with few trees or shrubs, such as pine barrens and oak savannas. It can only lay its eggs on lupine plants. (credit: modification of work by J & K Hollingsworth, USFWS)

After hatching, the larval caterpillars emerge and spend four to six weeks feeding solely on wild lupine (Figure 1.1.3). The caterpillars pupate (undergo metamorphosis) and emerge as butterflies after about four weeks. The adult butterflies feed on the

nectar of flowers of wild lupine and other plant species. A researcher interested in studying Karner blue butterflies at the organismal level might, in addition to asking questions about egg laying, ask questions about the butterflies' preferred temperature (a physiological question) or the behavior of the caterpillars when they are at different larval stages (a behavioral question).



Figure 1.1.3: The wild lupine *Lupinus perennis* is the host plant for the Karner blue butterfly.

Video



In other words, the adaptations of species are generally a 'good fit' for their current habitat and other environmental conditions because of natural selection over time.

Population Ecology

A population is a group of interbreeding organisms that are members of the same species living in the same area at the same time. (Organisms that are all members of the same species are called conspecifics.) A population is identified, in part, by where it lives, and its area of population may have natural or artificial boundaries: natural boundaries might be rivers, mountains, or deserts, while examples of artificial boundaries include mowed grass, manmade structures, or roads. The study of population ecology focuses on the number of individuals in an area and how and why population size changes over time. Population ecologists are particularly interested in counting the Karner blue butterfly, for example, because it is classified as federally endangered. However, the distribution and density of this species is highly influenced by the distribution and abundance of wild lupine. Researchers might ask questions about the factors leading to the decline of wild lupine and how these affect Karner blue butterflies. For example, ecologists know that wild lupine thrives in open areas where trees and shrubs are largely absent. In natural settings, intermittent

wildfires regularly remove trees and shrubs, helping to maintain the open areas that wild lupine requires. Mathematical models can be used to understand how wildfire suppression by humans has led to the decline of this important plant for the Karner blue butterfly.

Community Ecology

A biological community consists of the different species within an area, typically a three-dimensional space, and the interactions within and among these species. Community ecologists are interested in the processes driving these interactions and their consequences. Questions about conspecific interactions often focus on competition among members of the same species for a limited resource. Ecologists also study interactions among various species; members of different species are called heterospecifics. Examples of heterospecific interactions include predation, parasitism, herbivory, competition, and pollination. These interactions can have regulating effects on population sizes and can impact ecological and evolutionary processes affecting diversity.

For example, Karner blue butterfly larvae form mutualistic relationships with ants. Mutualism is a form of a long-term relationship that has coevolved between two species and from which each species benefits. For mutualism to exist between individual organisms, each species must receive some benefit from the other as a consequence of the relationship. Researchers have shown that there is an increase in the probability of survival when Karner blue butterfly larvae (caterpillars) are tended by ants. This might be because the larvae spend less time in each life stage when tended by ants, which provides an advantage for the larvae. Meanwhile, the Karner blue butterfly larvae secrete a carbohydrate-rich substance that is an important energy source for the ants. Both the Karner blue larvae and the ants benefit from their interaction.

Ecosystem Ecology

Ecosystem ecology is an extension of organismal, population, and community ecology. The ecosystem is composed of all the biotic components (living things) in an area along with the abiotic components (non-living things) of that area. Some of the abiotic components include air, water, and soil. Ecosystem biologists ask questions about how nutrients and energy are stored and how they move among organisms and the surrounding atmosphere, soil, and water.

The Karner blue butterflies and the wild lupine live in an oak-pine barren habitat. This habitat is characterized by natural disturbance and nutrient-poor soils that are low in nitrogen. The availability of nutrients is an important factor in the distribution of the plants that live in this habitat. Researchers interested in ecosystem ecology could ask questions about the importance of limited resources and the movement of resources, such as nutrients, through the biotic and abiotic portions of the ecosystem.

Video



Career Connection

Ecologist

A career in ecology contributes to many facets of human society. Understanding ecological issues can help society meet the basic human needs of food, shelter, and health care. Ecologists can conduct their research in the laboratory and outside in natural

environments (Figure 1.1.4). These natural environments can be as close to home as the stream running through your campus or as far away as the hydrothermal vents at the bottom of the Pacific Ocean. Ecologists manage natural resources such as white-tailed deer populations *Odocoileus virginianus* for hunting or aspen *Populus* spp. timber stands for paper production. Ecologists also work as educators who teach children and adults at various institutions including universities, high schools, museums, and nature centers. Ecologists may also work in advisory positions assisting local, state, and federal policymakers to develop laws that are ecologically sound, or they may develop those policies and legislation themselves. To become an ecologist requires an undergraduate degree, usually in a natural science. The undergraduate degree is often followed by specialized training or an advanced degree, depending on the area of ecology selected. Ecologists should also have a broad background in the physical sciences, as well as a sound foundation in mathematics and statistics.



Figure 1.1.4: This landscape ecologist is releasing a black-footed ferret into its native habitat as part of a study. (credit: USFWS Mountain Prairie Region, NPS)

Additional Resource

Click on this link to hear from an ecologist about their career:

https://www.sciencelearn.org.nz/videos/43-what-s-an-ecologist

Video



We will be talking about this much more as we move further into the semester!

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- **44.1: The Scope of Ecology** by OpenStax is licensed CC BY 4.0.

1.2: History of Ecology

Ecology is a new science and considered as an important branch of biological science, having only become prominent during the second half of the 20th century.[1] Ecological thought is derivative of established currents in philosophy, particularly from ethics and politics.[2]

Its history stems all the way back to the 4th century. One of the first ecologists whose writings survive may have been Aristotle or perhaps his student, Theophrastus, both of whom had interest in many species of animals and plants. Theophrastus described interrelationships between animals and their environment as early as the 4th century BC.[3] Ecology developed substantially in the 18th and 19th century. It began with Carl Linnaeus and his work with the economy of nature.[4] Soon after came Alexander von Humboldt and his work with botanical geography.[5] Alexander von Humboldt and Karl Möbius then contributed with the notion of biocoenosis. Eugenius Warming's work with ecological plant geography led to the founding of ecology as a discipline.[6] Charles Darwin's work also contributed to the science of ecology, and Darwin is often attributed with progressing the discipline more than anyone else in its young history. Ecological thought expanded even more in the early 20th century.[7] Major contributions included: Eduard Suess' and Vladimir Vernadsky's work with the biosphere, Arthur Tansley's ecosystem, Charles Elton's *Animal Ecology*, and Henry Cowles ecological succession.[8]

Ecology influenced the social sciences and humanities. Human ecology began in the early 20th century and it recognized humans as an ecological factor. Later James Lovelock advanced views on earth as a macro-organism with the Gaia hypothesis.[9][10] Conservation stemmed from the science of ecology. Important figures and movements include Shelford and the ESA, National Environmental Policy act, George Perkins Marsh, Theodore Roosevelt, Stephen A. Forbes, and post-Dust Bowl conservation. Later in the 20th century world governments collaborated on man's effects on the biosphere and Earth's environment.

The history of ecology is intertwined with the history of conservation efforts, in particular the founding of the Nature Conservancy.[11]

18th and 19th-Century Ecological murmurs

Arcadian and Imperial Ecology

In the early Eighteenth century, preceding Carl Linnaeus, two rival schools of thought dominated the growing scientific discipline of ecology. First, Gilbert White a "parson-naturalist" is attributed with developing and endorsing the view of Arcadian ecology. Arcadian ecology advocates for a "simple, humble life for man" and a harmonious relationship with humans and nature.[12] Opposing the Arcadian view is Francis Bacon's ideology, "imperial ecology". Imperialists work "to establish through the exercise of reason and by hard work, man's dominance over nature".[12] Imperial ecologists also believe that man should become a dominant figure over nature and all other organisms as "once enjoyed in the Garden of Eden".[12] Both views continued their rivalry through the early eighteenth century until Carl Linnaeus's support of imperialism; and in short time due to Linnaeus's popularity, imperial ecology became the dominant view within the discipline.

Carl Linnaeus and Systema Naturae

Carl Linnaeus, a Swedish naturalist, is well known for his work with taxonomy but his ideas helped to lay the groundwork for modern ecology. He developed a two part naming system for classifying plants and animals. Binomial Nomenclature was used to classify, describe, and name different genera and species. The compiled editions of *Systema Naturae* developed and popularized the naming system for plants and animals in modern biology. Reid suggests "Linnaeus can fairly be regarded as the originator of systematic and ecological studies in biodiversity," due to his naming and classifying of thousands of plant and animal species. Linnaeus also influenced the foundations of Darwinian evolution, he believed that there could be change in or between different species within fixed genera. Linnaeus was also one of the first naturalists to place men in the same category as primates.[4]

The botanical geography and Alexander von Humboldt

Throughout the 18th and the beginning of the 19th century, the great maritime powers such as Britain, Spain, and Portugal launched many world exploratory expeditions to develop maritime commerce with other countries, and to discover new natural resources, as well as to catalog them. At the beginning of the 18th century, about twenty thousand plant species were known, versus forty thousand at the beginning of the 19th century, and about 300,000 today.

These expeditions were joined by many scientists, including botanists, such as the German explorer Alexander von Humboldt. Humboldt is often considered as father of ecology. He was the first to take on the study of the relationship between organisms and their environment. He exposed the existing relationships between observed plant species and climate, and described vegetation zones using latitude and altitude, a discipline now known as geobotany. Von Humboldt was accompanied on his expedition by the botanist Aimé Bonpland.

In 1856, the Park Grass Experiment was established at the Rothamsted Experimental Station to test the effect of fertilizers and manures on hay yields. This is the longest-running field experiment in the world.[5]

The notion of biocoenosis: Wallace and Möbius

Alfred Russel Wallace, contemporary and colleague of Darwin, was first to propose a "geography" of animal species. Several authors recognized at the time that species were not independent of each other, and grouped them into plant species, animal species, and later into communities of living beings or biocoenosis. The first use of this term is usually attributed to Karl Möbius in 1877, but already in 1825, the French naturalist Adolphe Dureau de la Malle used the term *societé* about an assemblage of plant individuals of different species.

Warming and the foundation of ecology as discipline

While Darwin focused exclusively on competition as a selective force, Eugen Warming devised a new discipline that took abiotic factors, that is drought, fire, salt, cold etc., as seriously as biotic factors in the assembly of biotic communities. Biogeography before Warming was largely of descriptive nature – faunistic or floristic. Warming's aim was, through the study of organism (plant) morphology and anatomy, i.e. adaptation, to explain why a species occurred under a certain set of environmental conditions. Moreover, the goal of the new discipline was to explain why species occupying similar habitats, experiencing similar hazards, would solve problems in similar ways, despite often being of widely different phylogenetic descent. Based on his personal observations in Brazilian cerrado, in Denmark, Norwegian Finnmark and Greenland, Warming gave the first university course in ecological plant geography. Based on his lectures, he wrote the book 'Plantesamfund', which was immediate translated to German, Polish and Russian, later to English as 'Oecology of Plants'. Through its German edition, the book had an immense effect on British and North American scientists like Arthur Tansley, Henry Chandler Cowles and Frederic Clements.[6]

Malthusian influence

Thomas Robert Malthus was an influential writer on the subject of population and population limits in the early 19th century. His works were very important in shaping the ways in which Darwin saw the world worked. Malthus wrote:

> *That the increase of population is necessarily limited by the means of subsistence,*
>
> *That population does invariably increase when the means of subsistence increase, and,*
>
> *That the superior power of population is repressed, and the actual population kept equal to the means of subsistence, by misery and vice.*[13]

In An Essay on the Principle of Population Malthus argues for the reining in of rising population through 2 checks: Positive and Preventive checks. The first raising death rates, the later lowers birthing rates.[14] Malthus also brings forth the idea that the world population will move past the sustainable number of people.[15] This form of thought still continues to influences debates on birth and marriage rates to this theory brought forth by Malthus.[16] The essay had a major influence on Charles Darwin and helped him to theories his theory of Natural Selection.[17] This struggle proposed by Malthusian thought not only influenced the ecological work of Charles Darwin, but helped bring about an economic theory of world of ecology.[18]

Darwinism and the science of ecology

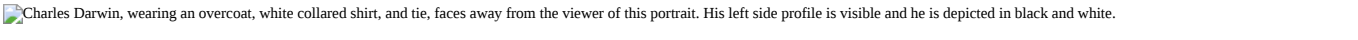

Charles Darwin, wearing an overcoat, white collared shirt, and tie, faces away from the viewer of this portrait. His left side profile is visible and he is depicted in black and white.

Figure 1.2.1: Julia Margaret Cameron's portrait of Darwin

It is often held that the roots of scientific ecology may be traced back to Darwin.[19] This contention may look convincing at first glance inasmuch as *On the Origin of Species* is full of observations and proposed mechanisms that clearly fit within the boundaries of modern ecology (e.g. the cat-to-clover chain – an ecological cascade) and because the term ecology was coined in 1866 by a

strong proponent of Darwinism, Ernst Haeckel. However, Darwin never used the word in his writings after this year, not even in his most "ecological" writings such as the foreword to the English edition of Hermann Müller's *The Fertilization of Flowers* (1883) or in his own treatise of earthworms and mull formation in forest soils (The formation of vegetable mould through the action of worms, 1881). Moreover, the pioneers founding ecology as a scientific discipline, such as Eugen Warming, A. F. W. Schimper, Gaston Bonnier, F.A. Forel, S.A. Forbes and Karl Möbius, made almost no reference to Darwin's ideas in their works.[7] This was clearly not out of ignorance or because the works of Darwin were not widespread. Some such as S.A.Forbes studying intricate food webs asked questions as yet unanswered about the instability of food chains that might persist if dominant competitors were not adapted to have self-constraint.[20] Others focused on the dominant themes at the beginning, concern with the relationship between organism morphology and physiology on one side and environment on the other, mainly abiotic environment, hence environmental selection. Darwin's concept of natural selection on the other hand focused primarily on competition.[21] The mechanisms other than competition that he described, primarily the divergence of character which can reduce competition and his statement that "struggle" as he used it was metaphorical and thus included environmental selection, were given less emphasis in the Origin than competition.[12] Despite most portrayals of Darwin conveying him as a non-aggressive recluse who let others fight his battles, Darwin remained all his life a man nearly obsessed with the ideas of competition, struggle and conquest – with all forms of human contact as confrontation.[12][22]

Although there is nothing incorrect in the details presented in the paragraph above, the fact that Darwinism used a particularly ecological view of adaptation and Haeckel's use and definitions of the term were steeped in Darwinism should not be ignored. According to ecologist and historian Robert P. McIntosh, "the relationship of ecology to Darwinian evolution is explicit in the title of the work in which ecology first appeared."[23][24] A more elaborate definition by Haeckel in 1870 is translated on the frontispiece of the influential ecology text known as 'Great Apes' as "… ecology is the study of all those complex interrelations referred to by Darwin as the conditions of the struggle for existence."[25][26] The issues brought up in the above paragraph are covered in more detail in the Early Beginnings section underneath that of History in the Wikipedia page on Ecology.

Early 20th century ~ Expansion of ecological thought

The biosphere – Eduard Suess and Vladimir Vernadsky

By the 19th century, ecology blossomed due to new discoveries in chemistry by Lavoisier and de Saussure, notably the nitrogen cycle. After observing the fact that life developed only within strict limits of each compartment that makes up the atmosphere, hydrosphere, and lithosphere, the Austrian geologist Eduard Suess proposed the term biosphere in 1875. Suess proposed the name biosphere for the conditions promoting life, such as those found on Earth, which includes flora, fauna, minerals, matter cycles, et cetera.

In the 1920s Vladimir I. Vernadsky, a Russian geologist who had defected to France, detailed the idea of the biosphere in his work "The biosphere" (1926), and described the fundamental principles of the biogeochemical cycles. He thus redefined the biosphere as the sum of all ecosystems.

First ecological damages were reported in the 18th century, as the multiplication of colonies caused deforestation. Since the 19th century, with the industrial revolution, more and more pressing concerns have grown about the impact of human activity on the environment. The term ecologist has been in use since the end of the 19th century.

The ecosystem: Arthur Tansley

Over the 19th century, botanical geography and zoogeography combined to form the basis of biogeography. This science, which deals with habitats of species, seeks to explain the reasons for the presence of certain species in a given location.

It was in 1935 that Arthur Tansley, the British ecologist, coined the term ecosystem, the interactive system established between the biocoenosis (the group of living creatures), and their biotope, the environment in which they live. Ecology thus became the science of ecosystems.

Tansley's concept of the ecosystem was adopted by the energetic and influential biology educator Eugene Odum. Along with his brother, Howard T. Odum, Eugene P. Odum wrote a textbook which (starting in 1953) educated more than one generation of biologists and ecologists in North America.

Ecological succession – Henry Chandler Cowles



Figure 1.2.2: The Indiana Dunes on Lake Michigan, which Cowles referred to in his development of his theories of ecological succession.

At the turn of the 20th century, Henry Chandler Cowles was one of the founders of the emerging study of "dynamic ecology", through his study of ecological succession at the Indiana Dunes, sand dunes at the southern end of Lake Michigan. Here Cowles found evidence of ecological succession in the vegetation and the soil with relation to age. Cowles was very aware of the roots of the concept and of his (primordial) predecessors.[8] Thus, he attributes the first use of the word to the French naturalist Adolphe Dureau de la Malle, who had described the vegetation development after forest clear-felling, and the first comprehensive study of successional processes to the Finnish botanist Ragnar Hult (1881).

Animal Ecology - Charles Elton

20th century English zoologist and ecologist, Charles Elton, is commonly credited as “the father of animal ecology”.[27] Elton influenced by Victor Shelford's *Animal Communities in Temperate America* began his research on animal ecology as an assistant to his colleague, Julian Huxley, on an ecological survey of the fauna in Spitsbergen in 1921. Elton's most famous studies were conducted during his time as a biological consultant to the Hudson Bay Company to help understand the fluctuations in the company's fur harvests. Elton studied the population fluctuations and dynamics of snowshoe hare, Canadian lynx, and other mammals of the region. Elton is also considered the first to coin the terms, food chain and food cycle in his famous book *Animal Ecology*.[28] Elton is also attributed with contributing to disciplines of: invasion ecology, community ecology, and wildlife disease ecology.[29]

G. Evelyn Hutchinson - father of modern ecology

George “G” Evelyn Hutchinson was a 20th-century ecologist who is commonly recognized as the “Father of Modern Ecology”. Hutchinson is of English descent but spent most of professional career studying in New Haven, Connecticut at Yale University. Throughout his career, over six decades, Hutchinson contributed to the sciences of limnology, entomology, genetics, biogeochemistry, mathematical theory of population dynamics and many more.[30] Hutchinson is also attributed as being the first to infuse science with theory within the discipline of ecology.[31] Hutchinson was also one of the first credited with combining ecology with mathematics. Another major contribution of Hutchinson was his development of the current definition of an organism's “niche” – as he recognized the role of an organism within its community. Finally, along with his great impact within the discipline of ecology throughout his professional years, Hutchinson also left a lasting impact in ecology through his many students he inspired. Foremost among them were Robert H. MacArthur, who received his PhD under Hutchinson, and Raymond L. Lindemann, who finished his PhD dissertation during a fellowship under him. MacArthur became the leader of theoretical ecology and, with E. O. Wilson, developed island biography theory. Raymond Lindemann was instrumental in the development of modern ecosystem science.[32]

20th-Century transition to modern ecology

"What is ecology?" was a questioned that was asked in almost every decade of the 20th century.[33] Unfortunately, the answer most often was that it was mainly a point of view to be used in other areas of biology and also "soft," like sociology, for example, rather than "hard," like physics. Although autecology (essentially physiological ecology) could progress through the typical scientific method of observation and hypothesis testing, synecology (the study of animal and plant communities) and genecology (evolutionary ecology), for which experimentation was as limited as it was for, say, geology, continued with much the same inductive gathering of data as did natural history studies.[34] Most often, patterns, present and historical, were used to develop theories having explanatory power, but which had little actual data in support. Darwin's theory, as much as it is a foundation of modern biology, is a prime example.

G. E. Hutchinson, identified above as the "father of modern ecology," through his influence raised the status of much of ecology to that of a rigorous science. By shepherding of Raymond Lindemann's work on the trophic-dynamic concept of ecosystems through the publication process after Lindemann's untimely death,[35] Hutchinson set the groundwork for what became modern ecosystem science. With his two famous papers in the late1950s, "Closing remarks,"[36] and "Homage to Santa Rosalia,"[37] as they are now known, Hutchinson launched the theoretical ecology which Robert MacArthur championed.

Ecosystem science became rapidly and sensibly associated with the "Big Science"—and obviously "hard" science—of atomic testing and nuclear energy. It was brought in by Stanley Auerbach, who established the Environmental Sciences Division at Oak Ridge National Laboratory,[38] to trace the routes of radionulcides through the environment, and by the Odum brothers, Howard and Eugene, much of whose early work was supported by the Atomic Energy Commission.[39] Eugene Odum's textbook, *Fundamentals of Ecology*, has become something of a bible today. When, in the 1960s, the International Biological Program (IBP) took on an ecosystem character,[40] ecology, with its foundation in systems science, forever entered the realm of Big Science, with projects having large scopes and big budgets. Just two years after the publication of Rcahel Carson's *Silent Spring* in 1962, ecosystem ecology was trumpeted as THE science of the environment in a series of articles in a special edition of *BioScience*.[41]

Theoretical ecology took a different path to establish its legitimacy, especially at eastern universities and certain West Coast campuses.[42] It was the path of Robert MacArthur, who used simple mathematics in his "Three Influential Papers,[43][44][45] also published in the late 1950s, on population and community ecology. Although the simple equations of theoretical ecology at the time, were unsupported by data, they still were still deemed to be "heuristic." They were resisted by a number of traditional ecologists, however, whose complaints of "intellectual censorship" of studies that did not fit into the hypothetico-deductive structure of the new ecology might be seen as evidence of the stature to which the Hutchinson-MacArthur approach had risen by the 1970s.[46]

Timeline of ecologists

A list of founders, innovators and their significant contributions to ecology, from Romanticism onward.

Notable figure	Lifespan	Major contribution & citation
Antonie van Leeuwenhoek	1632–1723	First to develop concept of food chains
Carl Linnaeus	1707–1778	Influential naturalist, inventor of science on the economy of nature[64][65]
Alexander Humboldt	1769–1859	First to describe ecological gradient of latitudinal biodiversity increase toward the tropics [66] in 1807
Charles Darwin	1809–1882	Founder of the hypothesis of evolution by means of natural selection, founder of ecological studies of soils[67]
Elizabeth Catherine Thomas Carne	1817-1873	Geologist, mineralogist and philosopher who observed rural vs urban living, spatially and culturally, finding in country living the best attack on suffocating class divides, healthier living, and best access to natural education.[68][69]
Herbert Spencer	1820–1903	Early founder of social ecology, coined the phrase 'survival of the fittest'[64][70]
Karl Möbius	1825–1908	First to develop concept of ecological community, biocenosis, or living community[71][72][73]
Ernst Haeckel	1834–1919	Invented the term ecology, popularized research links between ecology and evolution
Victor Hensen	1835–1924	Invented term plankton, developed quantitative and statistical measures of productivity in the seas
Eugenius Warming	1841–1924	Early founder of Ecological Plant Geography[6]
Ellen Swallow Richards	1842–1911	Pioneer and educator who linked urban ecology to human health[74]
Stephen Forbes	1844–1930	Early founder of entomology and ecological concepts in 1887 [20][75]
Vito Volterra	1860–1940	Independently pioneered mathematical populations models around the same time as Alfred J. Lotka.[76][77]
Vladimir Vernadsky	1869–1939	Founded the biosphere concept
Henry C. Cowles	1869–1939	Pioneering studies and conceptual development in studies of ecological succession[78]
Jan Christiaan Smuts	1870–1950	Coined the term holism in a 1926 book *Holism and Evolution*.[79]
Arthur G. Tansley	1871–1955	First to coin the term ecosystem in 1936 and notable researcher[72][80][81]

Charles Christopher Adams	1873–1955	Animal ecologist, biogeographer, author of first American book on animal ecology in 1913, founded ecological energetics[82][83]
Friedrich Ratzel	1844–1904	German geographer who first coined the term biogeography in 1891.
Frederic Clements	1874–1945	Authored the first influential American ecology book in 1905[84]
Victor Ernest Shelford	1877–1968	Founded physiological ecology, pioneered food-web and biome concepts, founded The Nature Conservancy[85][86]
Alfred J. Lotka	1880–1949	First to pioneer mathematical populations models explaining trophic (predator-prey) interactions using logistic equation[87]
Henry Gleason	1882–1975	Early ecology pioneer, quantitative theorist, author, and founder of the individualistic concept of ecology[84][88]
Charles S. Elton	1900–1991	'Father' of animal ecology, pioneered food-web & niche concepts and authored influential *Animal Ecology* text[85][89]
G. Evelyn Hutchinson	1903–1991	Limnologist and conceptually advanced the niche concept[90][91][92]
Eugene P. Odum	1913–2002	Co-founder of ecosystem ecology and ecological thermodynamic concepts[81][85][93][94]
Howard T. Odum	1924–2002	Co-founder of ecosystem ecology and ecological thermodynamic concepts[81][85][93][94][95][96]
Robert MacArthur	1930–1972	Co-founder on Theory of Island Biogeography and innovator of ecological statistical methods[97]

Ecological Influence on the Social Sciences and Humanities

Human ecology

Human ecology began in the 1920s, through the study of changes in vegetation succession in the city of Chicago. It became a distinct field of study in the 1970s. This marked the first recognition that humans, who had colonized all of the Earth's continents, were a major ecological factor. Humans greatly modify the environment through the development of the habitat (in particular urban planning), by intensive exploitation activities such as logging and fishing, and as side effects of agriculture, mining, and industry. Besides ecology and biology, this discipline involved many other natural and social sciences, such as anthropology and ethnology, economics, demography, architecture and urban planning, medicine and psychology, and many more. The development of human ecology led to the increasing role of ecological science in the design and management of cities.

In recent years human ecology has been a topic that has interested organizational researchers. Hannan and Freeman (*Population Ecology of Organizations (1977)*, American Journal of Sociology) argue that organizations do not only adapt to an environment. Instead it is also the environment that selects or rejects populations of organizations. In any given environment (in equilibrium) there will only be one form of organization (isomorphism). Organizational ecology has been a prominent theory in accounting for diversities of organizations and their changing composition over time.

James Lovelock and the Gaia hypothesis

The Gaia theory, proposed by James Lovelock, in his work *Gaia: A New Look at Life on Earth*, advanced the view that the Earth should be regarded as a single living macro-organism. In particular, it argued that the ensemble of living organisms has jointly evolved an ability to control the global environment — by influencing major physical parameters as the composition of the atmosphere, the evaporation rate, the chemistry of soils and oceans — so as to maintain conditions favorable to life. The idea has been supported by Lynn Margulis who extended her endosymbiotic theory which suggests that cell organelles originated from free living organisms to the idea that individual organisms of many species could be considered as symbionts within a larger metaphorical "super-organism".[98]

This vision was largely a sign of the times, in particular the growing perception after the Second World War that human activities such as nuclear energy, industrialization, pollution, and overexploitation of natural resources, fueled by exponential population growth, were threatening to create catastrophes on a planetary scale, and has influenced many in the environmental movement since then.

History and relationship between ecology and conservation and environmental movements

Environmentalists and other conservationists have used ecology and other sciences (e.g., climatology) to support their advocacy positions. Environmentalist views are often controversial for political or economic reasons. As a result, some scientific work in ecology directly influences policy and political debate; these in turn often direct ecological research.

The history of ecology, however, should not be conflated with that of environmental thought. Ecology as a modern science traces only from Darwin's publication of Origin of Species and Haeckel's subsequent naming of the science needed to study Darwin's theory. Awareness of humankind's effect on its environment has been traced to Gilbert White in 18th-century Selborne, England.[12] Awareness of nature and its interactions can be traced back even farther in time.[9][10] Ecology before Darwin, however, is analogous to medicine prior to Pasteur's discovery of the infectious nature of disease. The history is there, but it is only partly relevant.

Neither Darwin nor Haeckel, it is true, did self-avowed ecological studies. The same can be said for researchers in a number of fields who contributed to ecological thought well into the 1940s without avowedly being ecologists.[1][99] Raymond Pearl's population studies are a case in point.[100] Ecology in subject matter and techniques grew out of studies by botanists and plant geographers in the late 19th and early 20th centuries that paradoxically lacked Darwinian evolutionary perspectives. Until Mendel's studies with peas were rediscovered and melded into the Modern Synthesis,[101] Darwinism suffered in credibility. Many early plant ecologists had a Lamarckian view of inheritance, as did Darwin, at times. Ecological studies of animals and plants, preferably live and in the field, continued apace however.[102]

Conservation and environmental movements - 20th Century

When the Ecological Society of America (ESA) was chartered in 1915, it already had a conservation perspective.[103] Victor E. Shelford, a leader in the society's formation, had as one of its goals the preservation of the natural areas that were then the objects of study by ecologists, but were in danger of being degraded by human incursion.[104] Human ecology had also been a visible part of the ESA at its inception, as evident by publications such as: "The Control of Pneumonia and Influenza by the Weather," "An Overlook of the Relations of Dust to Humanity," "The Ecological Relations of the Polar Eskimo," and "City Street Dust and Infectious Diseases," in early pages of Ecology and Ecological Monographs. The ESA's second president, Ellsworth Huntington, was a human ecologist. Stephen Forbes, another early president, called for "humanizing" ecology in 1921, since man was clearly the dominant species on the Earth.[105]

This auspicious start actually was the first of a series of fitful progressions and reversions by the new science with regard to conservation. Human ecology necessarily focused on man-influenced environments and their practical problems. Ecologists in general, however, were trying to establish ecology as a basic science, one with enough prestige to make inroads into Ivy League faculties. Disturbed environments, it was thought, would not reveal nature's secrets.

Interest in the environment created by the American Dust Bowl produced a flurry of calls in 1935 for ecology to take a look at practical issues. Pioneering ecologist C. C. Adams wanted to return human ecology to the science.[106] Frederic E. Clements, the dominant plant ecologist of the day, reviewed land use issues leading to the Dust Bowl in terms of his ideas on plant succession and

climax.[107] Paul Sears reached a wide audience with his book, *Deserts on the March*.[108] World War II, perhaps, caused the issue to be put aside.

The tension between pure ecology, seeking to understand and explain, and applied ecology, seeking to describe and repair, came to a head after World War II. Adams again tried to push the ESA into applied areas by having it raise an endowment to promote ecology. He predicted that "a great expansion of ecology" was imminent "because of its integrating tendency."[109] Ecologists, however, were sensitive to the perception that ecology was still not considered a rigorous, quantitative science. Those who pushed for applied studies and active involvement in conservation were once more discreetly rebuffed. Human ecology became subsumed by sociology. It was sociologist Lewis Mumford who brought the ideas of George Perkins Marsh to modern attention in the 1955 conference, "Man's Role in Changing the Face of the Earth." That prestigious conclave was dominated by social scientists. At it, ecology was accused of "lacking experimental methods" and neglecting "man as an ecological agent." One participant dismissed ecology as "archaic and sterile."[110] Within the ESA, a frustrated Shelford started the Ecologists' Union when his Committee on Preservation of Natural Conditions ceased to function due to the political infighting over the ESA stance on conservation.[103] In 1950, the fledgling organization was renamed and incorporated as the Nature Conservancy, a name borrowed from the British government agency for the same purpose.

Two events, however, brought ecology's course back to applied problems. One was the Manhattan Project. It had become the Nuclear Energy Commission after the war. It is now the Department of Energy (DOE). Its ample budget included studies of the impacts of nuclear weapon use and production. That brought ecology to the issue, and it made a "Big Science" of it.[12][111] Ecosystem science, both basic and applied, began to compete with theoretical ecology (then called evolutionary ecology and also mathematical ecology). Eugene Odum, who published a very popular ecology textbook in 1953, became the champion of the ecosystem. In his publications, Odum called for ecology to have an ecosystem and applied focus.[112]

The second event was the publication of Silent Spring. Rachel Carson's book brought ecology as a word and concept to the public. Her influence was instant. A study committee, prodded by the publication of the book, reported to the ESA that their science was not ready to take on the responsibility being given to it.[113]

Carson's concept of ecology was very similar to Gene Odum's.[114] As a result, ecosystem science dominated the International Biological Program of the 1960s and 1970s, bringing both money and prestige to ecology.[115][116] Silent Spring was also the impetus for the environmental protection programs that were started in the Kennedy and Johnson administrations and passed into law just before the first Earth Day. Ecologists' input was welcomed. Former ESA President Stanley Cain, for example, was appointed an Assistant Secretary in the Department of the Interior.

The environmental assessment requirement of the 1969 National Environmental Policy Act (NEPA), "legitimized ecology," in the words of one environmental lawyer.[117] An ESA President called it "an ecological 'Magna Carta.'"[118] A prominent Canadian ecologist declared it a "boondoggle."[119] NEPA and similar state statutes, if nothing else, provided much employment for ecologists. Therein was the issue. Neither ecology nor ecologists were ready for the task. Not enough ecologists were available to work on impact assessment, outside of the DOE laboratories, leading to the rise of "instant ecologists,"[120] having dubious credentials and capabilities. Calls began to arise for the professionalization of ecology. Maverick scientist Frank Egler, in particular, devoted his sharp prose to the task.[121] Again, a schism arose between basic and applied scientists in the ESA, this time exacerbated by the question of environmental advocacy. The controversy, whose history has yet to receive adequate treatment, lasted through the 1970s and 1980s, ending with a voluntary certification process by the ESA, along with lobbying arm in Washington.[122]

Post-Earth Day, besides questions of advocacy and professionalism, ecology also had to deal with questions having to do with its basic principles. Many of the theoretical principles and methods of both ecosystem science and evolutionary ecology began to show little value in environmental analysis and assessment.[123] Ecologist, in general, started to question the methods and logic of their science under the pressure of its new notoriety.[84][124][125] Meanwhile, personnel with government agencies and environmental advocacy groups were accused of religiously applying dubious principles in their conservation work.[126] Management of endangered Spotted Owl populations brought the controversy to a head.[127]

Conservation for ecologists created travails paralleling those nuclear power gave former Manhattan Project scientists. In each case, science had to be reconciled with individual politics, religious beliefs, and worldviews, a difficult process. Some ecologists managed to keep their science separate from their advocacy; others unrepentantly became avowed environmentalists.[128]

Roosevelt & American conservation

Theodore Roosevelt was interested in nature from a young age. He carried his passion for nature into his political policies. Roosevelt felt it was necessary to preserve the resources of the nation and its environment. In 1902 he created the federal reclamation service, which reclaimed land for agriculture. He also created the Bureau of Forestry. This organization, headed by Gifford Pinchot, was formed to manage and maintain the nations timberlands.[129] Roosevelt signed the Act for the Preservation of American Antiquities in 1906. This act allowed for him to "declare by public proclamation historic landmarks, historic and prehistoric structures, and other objects of historic and scientific interest that are situated upon lands owned or controlled by the Government of the United States to be national monuments." Under this act he created up to 18 national monuments. During his presidency, Roosevelt established 51 Federal Bird Reservations, 4 National Game Preserves, 150 National Forests, and 5 National Parks. Overall he protected over 200 million acres of land.[130]

Ecology and global policy

Ecology became a central part of the World's politics as early as 1971, UNESCO launched a research program called *Man and Biosphere*, with the objective of increasing knowledge about the mutual relationship between humans and nature. A few years later it defined the concept of Biosphere Reserve.

In 1972, the United Nations held the first international Conference on the Human Environment in Stockholm, prepared by Rene Dubos and other experts. This conference was the origin of the phrase "Think Globally, Act Locally". The next major events in ecology were the development of the concept of biosphere and the appearance of terms "biological diversity"—or now more commonly biodiversity—in the 1980s. These terms were developed during the Earth Summit in Rio de Janeiro in 1992, where the concept of the biosphere was recognized by the major international organizations, and risks associated with reductions in biodiversity were publicly acknowledged.

Then, in 1997, the dangers the biosphere was facing were recognized all over the world at the conference leading to the Kyoto Protocol. In particular, this conference highlighted the increasing dangers of the greenhouse effect – related to the increasing concentration of greenhouse gases in the atmosphere, leading to global changes in climate. In Kyoto, most of the world's nations recognized the importance of looking at ecology from a global point of view, on a worldwide scale, and to take into account the impact of humans on the Earth's environment.

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1.3: Subdisciplines of Ecology

Learning Objectives

- Appreciate the diversity of ecological studies
- Understand how ecology interacts with other fields

Subdisciplines of ecology, and subdiscipline classification

Ecology is a broad discipline comprising many subdisciplines. The field of ecology can be subdivided according to several classification schemes (each includes examples and is not comprehensive by any means):

By methodology used for investigation

- Field ecology – Collection of information outside a laboratory, library or workplace setting
- Quantitative ecology – the application of advanced mathematical and statistical tools to any number of problems in the field of ecology
- Theoretical ecology – the development of ecological theory, usually with mathematical, statistical and/or computer modeling tools.

By spatial scale of ecological system under study

- Global ecology – The global sum of all ecosystems on Earth
- Macroecology – Study of relationships between organisms and their environment at large spatial scales
- Microecology – Microbial ecology or ecology of a microhabitat

By level of organisation or scope

Arranged from lowest to highest level of organisation:[1]

- Autecology – the study of individual organisms of a single species in relation to their environment
- Synecology – the study of homogenous or heterogenous groups of organisms in relation to their environment
  - Population ecology – Study of the dynamics of species populations and how these populations interact with the environment – the study of homogenous groups of organisms related as a single species
  - Community ecology – Associated populations of species in a given area – the study of heterogenous groups of organisms comprised of multiple associated species
  - Ecosystem ecology – Study of living and non-living components of ecosystems and their interactions

By biological classification or taxon under study

- Human ecology – Study of the relationship between humans and their natural, social, and built environments
- Animal ecology – Scientific study of the relationships between living animals and their environment
- Insect ecology – The study of how insects interact with the surrounding environment
- Microbial ecology – Study of the relationship of microorganisms with their environment
- Plant ecology – The study of effect of the environment on the abundance and distribution of plants.

By biome under study

- Benthic ecology – The study of the interaction of sea-floor organisms with each other and with the environment
- Desert ecology – The study of interactions between both biotic and abiotic components of desert environments
- Forest ecology – Study of interactions between the biota and environment in forests
- Grassland ecology – Area with vegetation dominated by grasses
- Marine ecology – The study of the interactions between organisms and environment in the sea
- Aquatic ecology – The study of interactions between organisms and the environment in water
- Urban ecology – Study of the relation of living organisms with each other and their surroundings in the context of an urban environment

By biogeographic realm or climatic area under study

- Arctic ecology – The study of the relationships between biotic and abiotic factors in the arctic
- Polar ecology – The relationship between plants and animals and a polar environment
- Tropical ecology – The study of the relationships between the biotic and abiotic components of the tropics.

By ecological aspects or phenomena under investigation

- Behavioral ecology – Study of the evolutionary basis for animal behavior due to ecological pressures
- Chemical ecology – Study of chemically-mediated interactiond between living organisms – which deals with the ecological role of biological chemicals used in a wide range of areas including defense against predators and attraction of mates
- Disease ecology – Sub-discipline of ecology – which studies host-pathogen interactions, particularly those of infectious diseases, within the context of environmental factors;
- Ecophysiology – Study of adaptation of an organism's physiology to environmental conditions – which studies the interaction of physiological traits with the abiotic environment
- Ecotoxicology – which looks at the ecological role of toxic chemicals (often pollutants, but also naturally occurring compounds)
- Evolutionary ecology – Interaction of biology and evolution – or ecoevolution which looks at evolutionary changes in the context of the populations and communities in which the organisms exist
- Fire ecology – Study of fire in ecosystems – which looks at the role of fire in the environment of plants and animals and its effect on ecological communities
- Functional ecology – the study of the roles, or functions, that certain species (or groups thereof) play in an ecosystem
- Genetic ecology – Study of genetic material in the environment
- Landscape ecology – Science of relationships between ecological processes in the environment and particular ecosystems
  - Landscape limnology – Spatially explicit study of lakes, streams, and wetlands as they interact with freshwater, terrestrial, and human landscapes to determine the effects of pattern on ecosystem processes across temporal and spatial scales
- Molecular ecology – A field of evolutionary biology that applies molecular population genetics, molecular phylogenetics, and genomics to traditional ecological questions –
- Paleoecology – Study of interactions between organisms and their environments across geologic timescales
- Social ecology – Study of relationships between people and their environment
- Soil ecology – the ecology of the pedosphere
- Spatial ecology – Study of the distribution or space occupied by species
- Thermal ecology – the study of the relationship between temperature and organisms.

Ecology-involved interdisciplinary fields

- Agroecology – Study of ecological processes in agriculture
- Applied ecology – the practice of employing ecological principles and understanding to solve real world problems (includes agroecology and conservation biology);
  - Conservation ecology – Study of threats to biological diversity – which studies how to reduce the risk of species extinction
  - Restoration ecology – Scientific study of renewing and restoring ecosystems – which attempts to understand the ecological basis needed to restore impaired or damaged ecosystems
- Biogeochemistry – Study of chemical cycles of the earth that are either driven by or influence biological activity
- Biogeography – Study of the distribution of species and ecosystems in geographic space and through geological time
- Ecological design – Design that minimizes environmentally destructive impacts by integrating itself with living processes
- Ecological economics – Interdependence of human economies and natural ecosystems
- Ecological engineering – Environmental engineering
- Ecological anthropology – Study of cultural adaptations to environments
  - Festive ecology – Study of the relationships between the symbolism and the ecology of the plants, fungi and animals associated with cultural events
- Ecological health
- Ecosophy – Philosophy of ecological harmony or equilibrium as developed by Arne Næss or Félix Guattari

- Environmental psychology – Academic study of the mind's relationship to one's immediate surroundings
- Natural history – Study of organisms including plants or animals in their environment
- Systems ecology – Holistic approach to the study of ecological systems

Other disciplines

Ecology has also inspired (and lent its name to) other non-biological disciplines such as:

- Media ecology
- Industrial ecology
- Information ecology

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1.4: An Overview of Essential Mathematics Used in Science

Math, Statistics, and Science

Mathematics is the abstract science of numbers, quantity and space. Mathematics may be studied in its own right (pure mathematics), or as it is applied to scientific disciplines such as (applied mathematics).

Statistics is a mathematical body of science that pertains to the collection, analysis, interpretation or explanation, and presentation of data, or as a branch of mathematics.

Mathematics and statistics are vital for scientific inquiry. It is an especially imperative tool for disciplines that are inherently variable and require an extensive collection of data. Ideally, scientists would like to collect data from every individual in the population of interest, but this is rarely possible. As a result, scientists often must use data collected from a representative sample of individuals to draw inferences about basic biological phenomena for a population. This is where mathematics and statistics step into the party.

Math and Ecology

Quantitative ecology is the application of advanced mathematical and statistical tools to any number of problems in the field of ecology. It is a small but growing subfield in ecology, reflecting the demand among practicing ecologists to interpret ever larger and more complex data sets using quantitative reasoning. Quantitative ecologists might apply some combination of deterministic or stochastic mathematical models to theoretical questions or they might use sophisticated methods in applied statistics for experimental design and hypothesis testing. Typical problems in quantitative ecology include estimating the dynamics and status of wild populations, modeling the impacts of anthropogenic or climatic change on ecological communities, and predicting the spread of invasive species or disease outbreaks.

Quantitative ecology, which mainly focuses on statistical and computational methods for addressing applied problems, is distinct from **theoretical ecology** which tends to explore focus on understanding the dynamics of simple mechanistic models and their implications for a general set of biological systems using mathematical arguments.

Why Statistics?

Some of the most important functions of statistics include:

- Description and summary of basic findings (Descriptive statistics).
- Testing hypotheses regarding relationships between variables so the cause and effect can begin to be understood (inferential statistics).
- Presenting findings in an easily understood manner – misunderstandings keep science from moving progressing!

Essential Mathematical Terms and Concepts

General terms:

- Data – Systematically recorded information.
- Value – Each measurement or observation
- Variable – The object being controlled, manipulated, measured or observed. There are two main types:
  - Independent (explanatory) – The variable that you think will affect what is being measured/observed.
  - Dependent (response) – The variable that is being measured.
- Population – Entire set of objects to be studied.
  - Parameter – Numerical characteristic of population.
- Sample – Sub-collection of objects from population.
  - Statistic – Numerical characteristic of sample from population.

Example 1.4.1

You are a biologist who studies how monarch butterfly (*Danaus plexippus*) populations are affected by habitat destruction. You set up a long-term study to monitor populations in degraded, intact, and restored habitats where monarchs historically have been recorded/observed.

- Population: All monarch butterflies.
- Parameter: Not possible to collect a population worth of data for monarchs. Thus, no parameters can be calculated.
- Sample: Total monarchs observed at each field site during each year of the study.
- Statistic: Any calculations/manipulations from the field site data.

Types of statistics:

- Descriptive statistics – Are calculations to summarize trends in the data. Minimally, measures of center (averages) and spread (standard deviations) from data recorded.
- Inferential statistics – The point of inferential statistics is to take data from the sample to make inferences about the population. Calculations here test hypotheses and try to find/infer cause and effect relationships and/or correlations.

It is important to note that statistics can only be helpful if the data from the sample is representative of the population and the interpretation of the data is unbiased!

Types of data:

- Qualitative (categorical) data – Data expressed not in terms of numbers, but rather by means of a natural language description. There are two main types of qualitative data:
  - Ordinal – When categories are in a particular order (ex: large, medium, small)
  - Nominal – When categories have no natural ordering (ex: dog breed, color)
  - Graph types used: Pie, bar
- Quantitative (numerical) data – Data expressed not by means of a natural language description, but rather in terms of numbers. There are two main types of quantitative data:
  - Continuous – Numbers where any integer or fraction can be observed (ex: time, height, or weight)
  - Discrete – A fixed number of outcomes is possible such that there are only whole integers possible (ex: counts)
  - Graph types used: Histograms, line-graphs, scatterplots

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1.5: Summarizing Data - Descriptive Statistics

How do you summarize data?

Data is summarized in two main ways: summary calculations and summary visualizations

Calculations: What types of measures are used?

To be able to interpret patterns in the data, raw data must first be manipulated and summarized into two categories of measurements: Measures of central tendency and measures of variability. These two categories of measurements encapsulate the first step of scientific inquiry, descriptive statistics.

Measures of central tendency (center) – Provides information of how data cluster around some single middle value. While there are several ways to measure central tendency, the two measures most often used in Ecology are the mean and the median:

- **Mean** (average) – Sum of all individual values (Σx_i) divided by total number of values in sample/population (n). This is the most commonly used measure of central tendency under symmetrical (normal) distribution. It is sensitive to outliers. The sample mean is usually denoted $\bar{x}$.
- **Median** – The middle value when the data set is ordered in sequential rank. This is commonly used when data is skewed and is resistant to outliers. Notice that if there is an even number of values, the median is calculated by adding the middle two values, and dividing by 2 :

  for an odd number of values, ranked smallest to largest: 1, 3, 3, **6**, 7, 8, 9. The median is **6**.

  for an even number of values, ranked smallest to largest: 1, 2, 3, **4, 5**, 6, 7, 9. The median is $(4 + 5) \div 2 \ = 4.5$.

- **Mode** – The most frequently occurring value in the sample. This is less often used in Ecology.

Measures of variability (spread) – Describes how spread out or dispersed the data are. There are two main measures of spread used in biological inquiry:

- **Range** – Quantifies the distance between the largest and smallest data values.
- **Standard deviation** – Quantifies the variation or dispersion from the average of a dataset. A low standard deviation indicates that the data tends to be very close to the mean; a high standard deviation indicates that the data points are spread out over a large range of values. This calculation is sensitive to outliers. The standard deviation of a sample is denoted with a lower case ***s*** and is calculated as follows:

$$s = \sqrt{\frac{(x_i - \bar{x})^2}{n-1}} \tag{1.5.1}$$

  Notice that the numerator in the formula for the standard deviation includes the term $(x_i - \bar{x})$ which measures how far each individual value (x_i) is from the sample mean $\bar{x}$. If the data are highly dispersed/variable, some of these values will be larger, and hence the standard deviation will be large.

- **Standard error (SE)** – Quantifies how different the sample mean (the average of the data values you have) is likely to be from the mean for the whole population mean (i.e., what you are trying to estimate). It tells you how much the sample mean would vary if you were to repeat a study using new samples from within a single population. The standard error is calculated by dividing the standard deviation by the square root of the sample size:

$$SE = \frac{s}{\sqrt{n}} \tag{1.5.2}$$

Visualizing the data: How are tables and graphs used?

After all desired descriptive statistics are calculated, they are typically visually summarized into either a table or graph.

Tables:

A **table** is a set of data values arranged into columns and rows. Typically the columns encompass a broad data category, and the rows encompass another. Within each broad category, there are subcategories that determine how many columns and rows the table

consists of. Tables are used to both collect and summarize data. However, most of the time when tables are presented, they consist of summarized data, not raw data. Although tables allow summarized data to be presented in an orderly manner, most people prefer to translate tables into the more powerful data visualization tool, a graph.

Graphs:

A **graph** is a diagram showing the relation between variable quantities, typically of two variables, each measured along one of a pair of axes at right angles. Graphs can look like a chart or drawing. Most graphs use bars, lines, or parts of a circle to display data. However, there are sometimes when graphs are overlaid on top of maps to also display geographical location, or are even animated to be interactive.

Major graph type categories:

- **Circle/Pie** – A circular chart divided into slices to illustrate numerical proportion. In a pie chart, the arc length of each slice (and consequently its central angle and area), is proportional to the quantity it represents. While it is named for its resemblance to a pie that has been sliced, there are variations on the way it can be presented.
- **Line** – A type of chart which displays information as a series of data points called 'markers' connected by straight line segments. It is a basic type of chart common in many fields. It is similar to a scatter plot except that the measurement points are ordered in sequence (typically by their x-axis value) and joined with straight line segments. A line chart is often used to visualize a trend in data over intervals of time – a time series – thus the line is often drawn chronologically.

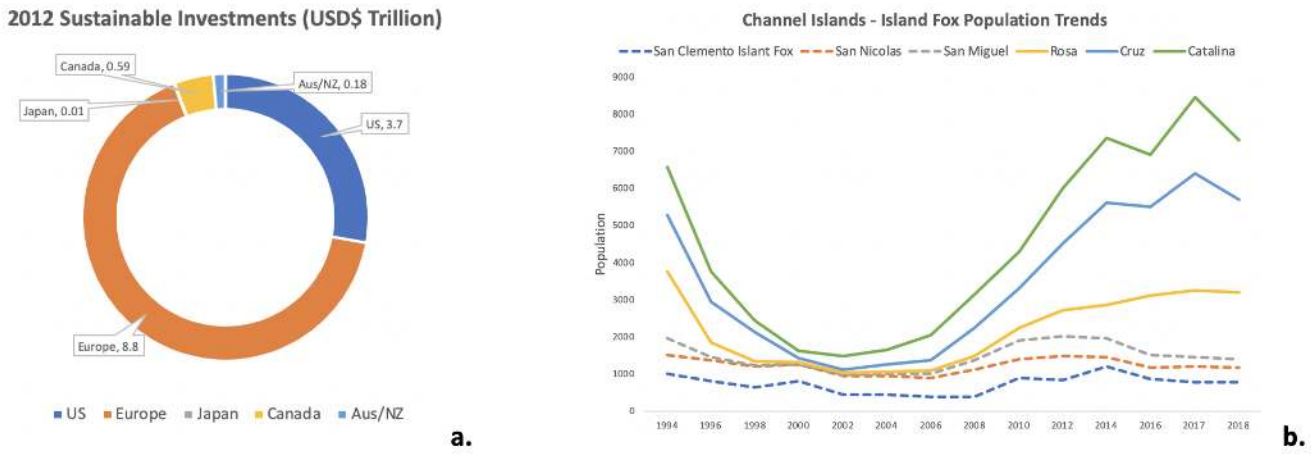


Figure 1.5.1**:** Examples of a circle/pie graph (a.) and a line graph (b.). Image created by Rachel Schleiger (CC-BY-NC).

- **Scatter plot** – Is a graph in which the values of two variables are plotted along the horizontal and vertical axes, the pattern of the resulting points revealing any correlation preset. The data are displayed as a collection of points, each having the value of one variable determining the position on the horizontal axis and the value of the other variable determining the position on the vertical axis.

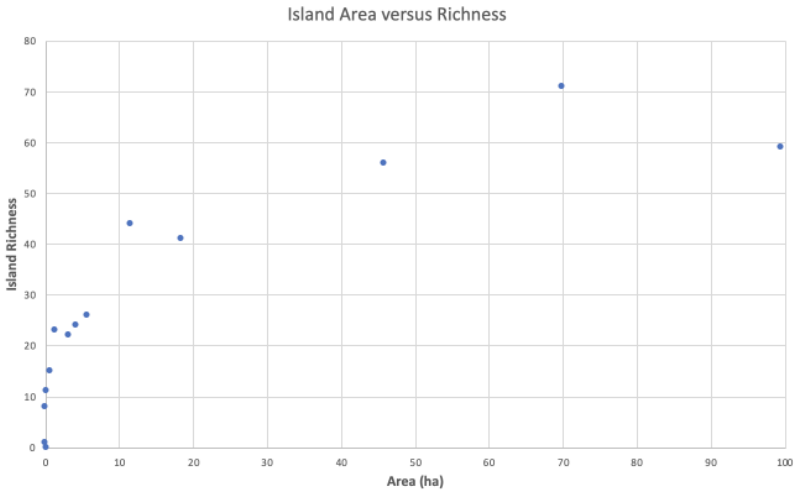


Figure 1.5.2**:** Example of a scatter plot. Image created by Rachel Schleiger (CC-BY-NC).

- **Bar** – A chart or graph that presents categorical data with rectangular bars with heights or lengths proportional to the values that they represent. The bars can be plotted vertically or horizontally.
- **Histogram** – Is an approximate representation of the distribution of numerical data. To construct a histogram, the first step is to "bin" (or "bucket") the range of values—that is, divide the entire range of values into a series of intervals—and then count how many values fall into each interval. The bins are usually specified as consecutive, non-overlapping intervals of a variable. The bins (intervals) must be adjacent (meaning there are not spaces between them like there are in bar graphs), and are often (but not required to be) of equal size. If the bins are of equal size, a rectangle is erected over the bin with height proportional to the frequency—the number of cases in each bin.

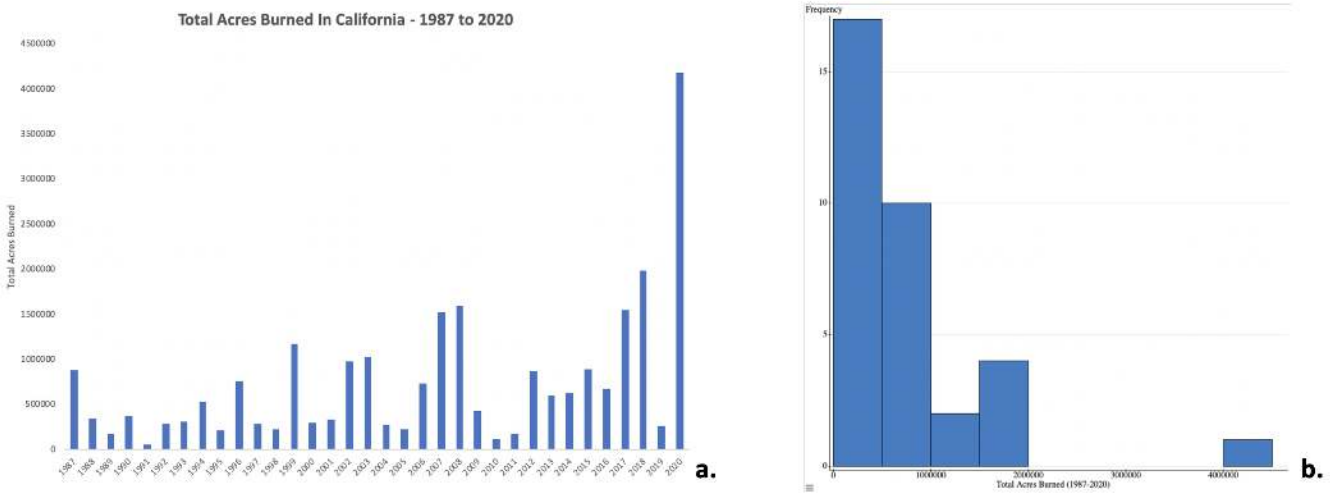


Figure 1.5.3**:** Examples of a bar graph (a.) and a histogram (b.) using the same dataset. Image created by Rachel Schleiger (CC-BY-NC).

Characteristics of effective graphical displays

> *The greatest value of a picture is when it forces us to notice what we never expected to see.*

Graphics *reveal* data. Indeed graphics can be more precise and revealing than conventional statistical computations."[3]

In his 1983 book *The Visual Display of Quantitative Information*, Edward Tufte defines 'graphical displays' and principles for effective graphical display in the following passage: "Excellence in statistical graphics consists of complex ideas communicated with clarity, precision, and efficiency.

Professor Tufte explained that users of information displays are executing particular *analytical tasks* such as making comparisons. The *design principle* of the information graphic should support the analytical task.[1] As William Cleveland and Robert McGill show, different graphical elements accomplish this more or less effectively. For example, dot plots and bar charts outperform pie charts.[12]

Graphical displays should:

- show the data
- induce the viewer to think about the substance rather than about methodology, graphic design, the technology of graphic production, or something else
- avoid distorting what the data has to say
- present many numbers in a small space
- make large data sets coherent
- encourage the eye to compare different pieces of data
- reveal the data at several levels of detail, from a broad overview to the fine structure
- serve a reasonably clear purpose: description, exploration, tabulation, or decoration
- be closely integrated with the statistical and verbal descriptions of a data set.

Additional Resource

Explore data visualizations at from data to viz.

1. *techatstate (7 August 2013). "Tech@State: Data Visualization - Keynote by Dr Edward Tufte". Archived from the original on 29 March 2017. Retrieved 29 November 2016 – via YouTube.*
2. *leveland, W. S.; McGill, R. (1985). "Graphical perception and graphical methods for analyzing scientific data". Science. **229** (4716): 828–33. Bibcode:1985Sci...229..828C. doi:10.1126/science.229.4716.828. PMID 17777913. S2CID 16342041.*
3. *Tufte, Edward (1983). The Visual Display of Quantitative Information. Cheshire, Connecticut: Graphics Press. ISBN 0-9613921-4-2. Archived from the original on 2013-01-14. Retrieved 2019-08-10.*

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1.6: Testing Hypotheses - Inferential Statistics

Scientific Hypotheses:

Biological (Scientific) hypothesis: An idea that proposes a tentative explanation about a phenomenon or a narrow set of phenomena observed in the natural world. This is the backbone of all scientific inquiry! As such it is important to have a solid biological hypothesis before moving forward in the scientific method (i.e. procedures, results, discussion). After the creation of a solid biological hypothesis, it can then be simplified into a statistical hypothesis (as defined below) that will become the basis for how the data will be analyzed and interpreted.

Statistical hypotheses: After defining a strong biological hypothesis, a statistical hypothesis can be created based on what you will predict will be the measured outcome(s) (dependent variable(s)). If a study has multiple measured outcomes there can be multiple statistical hypotheses. Each statistical hypothesis will have two components (Null and Alternative).

- **Null hypothesis** (Ho) –This hypothesis states that there is no relationship (or no pattern) between the independent and dependent variables.
- **Alternative hypothesis** (H1) – This hypothesis states that there is a relationship (or is a pattern) between the independent and dependent variables.

Variables

Independent versus dependent variables: For both biological and statistical hypotheses there should be two basic variables defined:

- **Independent (explanatory) variable** – It is usually what phenomena you think will affect the measure you are interested in (dependent variable).
- **Dependent (response) variable** – A dependent variable is what you measure in the experiment and what is affected during the experiment. The dependent variable responds to (depends on) the independent variable. In a scientific experiment, you cannot have a dependent variable without an independent variable.

Example 1.6.1

Yellow-billed Cuckoo nests were counted during breeding season in degraded, restored, and intact riparian habitats to see overall habitat preference for nesting sites increased with habitat health.

- Scientific hypothesis: Yellow-billed Cuckoo will have habitat preferences because of habitat health/status.
- Statistical hypotheses: (Ho) There will be no differences in number of nests between habitats with different health/status. (H1) There will be more nests in restored and intact habitats compared to degraded.
- Independent variable = Habitat health/status
- Dependent variable = Number of nests counted

Analysis and Conclusions

Finally, after defining the biological hypothesis, statistical hypothesis, and collecting all your data, a researcher can begin statistical analysis. A statistical test will mathematically “test” your data against the statistical hypothesis. The type of statistical test that is used depends on the type and quantity of variables in the study, as well as the question the researcher wants to ask. After computing the statistical test, the outcome will indicate which statistical hypothesis is more likely. This, in turn indicates to scientists what level of inference can be gained from the data compared to the biological hypothesis (the focus point of the study). Then a conclusion can be made based on the sample about the entire population. It is important to note that the process does not stop here. Scientists will want to continue to test this conclusion until a clear pattern emerges (or not) or to investigate similar but different questions.

Basic Statistical Tests

Inferential statistics generally provide a test statistic, the degrees of freedom (related to the number of individuals in each sample) and a p-value. Significance (acceptance of the alternative hypothesis) is generally based on the p-value. Depending on the field, scientists will often use a cut-off of 0.01 or 0.05 to determine significance. If the test returns a p-value that is less than this value, the relationship is deemed significant.

- **Chi-Square – Are two categorical variables related?**
  - (e.g. do different habitats different in the numbers of species of each type?)
- **T-Test – Does the mean (continuous data) of one group (a categorical variable) differ from the mean of another group?**
  - (e.g. are oak trees taller than hickory trees, on average?)
- **ANOVA – Does the mean of several groups differ? A post-hoc test is used to run pairwise comparisons if so**
  - (e.g. does height differ across tree species, on average?)
- **Linear regression - Are two continuous variables linearly related?**
  - (e.g. do taller trees have a larger circumference?)

Statistical Significance and Hypotheses

If $p \leq 0.05$ – accept the alternative hypothesis

- There is less than 5% chance that the samples are from the same population
- There is a significant difference between the samples

If $p > 0.05$ – accept the null hypothesis

- There is no significant difference between the samples

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CHAPTER OVERVIEW

Chapter 2: The Physical Environment

Learning Objectives

- Objective 1
- Objective 2
- Objective 3
- Objective 4

2.1: Properties of Water
2.2: Water (Hydrologic) Cycle
2.3: Soils
2.4: The Atmosphere
2.5: Earth's Energy Balance
2.6: Atmospheric and Oceanic Circulation
2.7: What Makes the Climate Change
2.8: Past Climate Change

Summary

Summary to be added

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2.1: Properties of Water

Do you ever wonder why scientists spend time looking for water on other planets? It is because water is essential to life, as we understand it; even minute traces of it on another planet can indicate that life could or did exist on that planet. Water is one of the more abundant molecules in living cells and the one most critical to life as we know it. Approximately 60–70 percent of your body is made up of water. Without it, life simply would not exist.

Water Is a Polar Molecule

The hydrogen and oxygen atoms within water molecules form polar covalent bonds. The shared electrons spend more time associated with the oxygen atom than they do with hydrogen atoms. There is no overall charge to a water molecule, but there is a slight positive charge on each hydrogen atom and a slight negative charge on the oxygen atom. Because of these charges, the slightly positive hydrogen atoms repel each other and form the unique shape seen in (Figure 2.1.1).

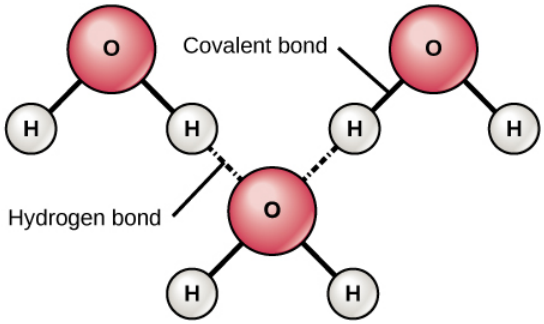


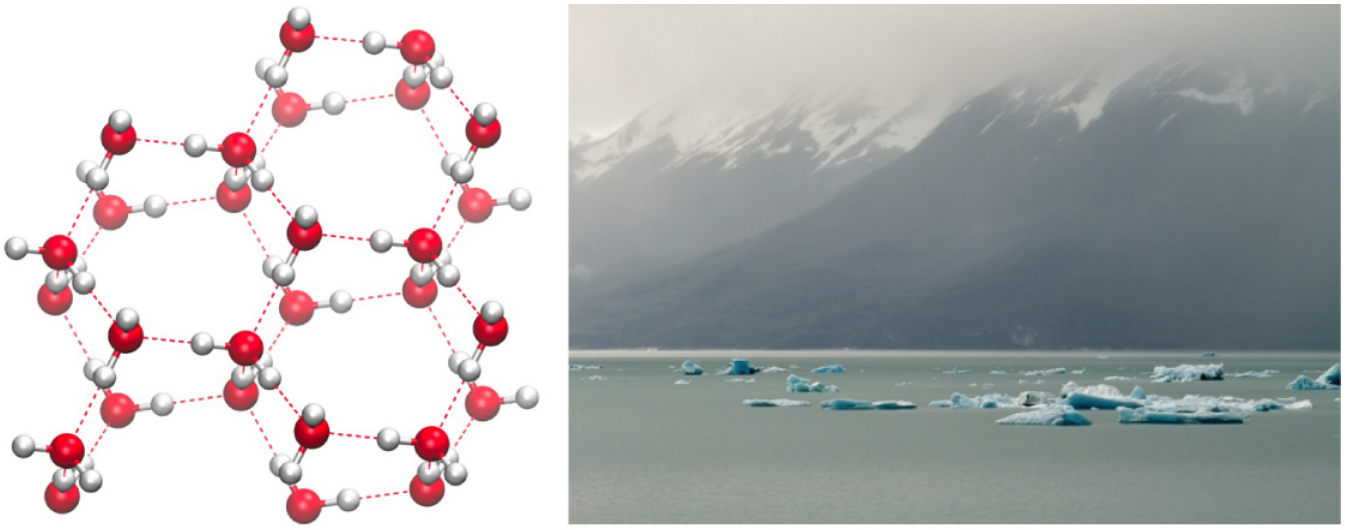
Figure 2.1.1**:** Hydrogen bonds form between slightly positive (δ+) and slightly negative (δ–) charges of polar covalent molecules, such as water.

Each water molecule attracts other water molecules because of the positive and negative charges in the different parts of the molecule allowing the formation of hydrogen bonds. Water also attracts and form hydrogen bonds with other polar molecules (such as sugars). When a substance readily forms hydrogen bonds with water, it can dissolve in water and is referred to as hydrophilic ("water-loving"). Hydrogen bonds are not readily formed with nonpolar substances like oils and fats. These nonpolar compounds are hydrophobic ("water-fearing") and will not dissolve in water.

Water Stabilizes Temperature

Temperature is a measure of the motion (kinetic energy) of molecules. As the motion increases, energy is higher and thus temperature is higher. Water absorbs a great deal of energy before its temperature rises. Increased energy disrupts the hydrogen bonds between water molecules. The hydrogen bonds in water allow it to absorb and release heat energy more slowly than many other substances (giving water a high specific heat). Because these bonds can be created and disrupted rapidly, water absorbs an increase in energy and temperature changes only minimally. This means that water moderates temperature changes within organisms and in their environments. As energy input continues, the balance between hydrogen-bond formation and destruction swings toward the destruction side. More bonds are broken than are formed. This process results in the release of individual water molecules at the surface of the liquid (such as a body of water, the leaves of a plant, or the skin of an organism) in a process called evaporation. Evaporation of sweat, which is 90 percent water, allows for cooling of an organism, because breaking hydrogen bonds requires an input of energy and takes heat away from the body.

Conversely, as molecular motion decreases and temperatures drop, less energy is present to break the hydrogen bonds between water molecules. These bonds remain intact and begin to form a rigid, lattice-like structure (e.g., ice) (Figure 2.1.2**a**). When frozen, ice is less dense than liquid water (the molecules are farther apart). This means that ice floats on the surface of a body of water (Figure 2.1.2**b**). In lakes, ponds, and oceans, ice will form on the surface of the water, creating an insulating barrier to protect the animal and plant life beneath from freezing in the water. If this did not happen, plants and animals living in water would freeze in a block of ice and could not move freely, making life in cold temperatures difficult or impossible.



(a) (b)

Figure 2.1.2**:**
(a) The lattice structure of ice makes it less dense than the freely flowing molecules of liquid water. Ice's lower density enables it to (b) float on water (credit a: modification of work by Jane Whitney; credit b: modification of work by Carlos Ponte).

CONCEPT IN ACTION

Click here to see a 3-D animation of the structure of an ice lattice. (credit: image created by Jane Whitney using Visual Molecular Dynamics (VMD) software (Humphrey et al, 1996)

Water Is an Excellent Solvent

Because water is a polar molecule, with slight positive and negative charges, ionic compounds and polar molecules can readily dissolve in it. Water is, therefore, what is referred to as a solvent—a substance capable of dissolving another substance. The charged particles will form hydrogen bonds with a surrounding layer of water molecules. This is referred to as a sphere of hydration or hydration shells and serves to keep the particles separated or dispersed in the water. In the case of table salt (NaCl) mixed in water (Figure 2.1.3), the sodium and chloride ions separate, or dissociate, in the water, and spheres of hydration are formed around the ions. A positively charged sodium ion is surrounded by the partially negative charges of oxygen atoms in water molecules. A negatively charged chloride ion is surrounded by the partially positive charges of hydrogen atoms in water molecules. The polarity of the water molecule makes it an effective solvent and is important in its many roles in living systems (i.e. cell transport, secretion of waste products, nutrient absorbtion).

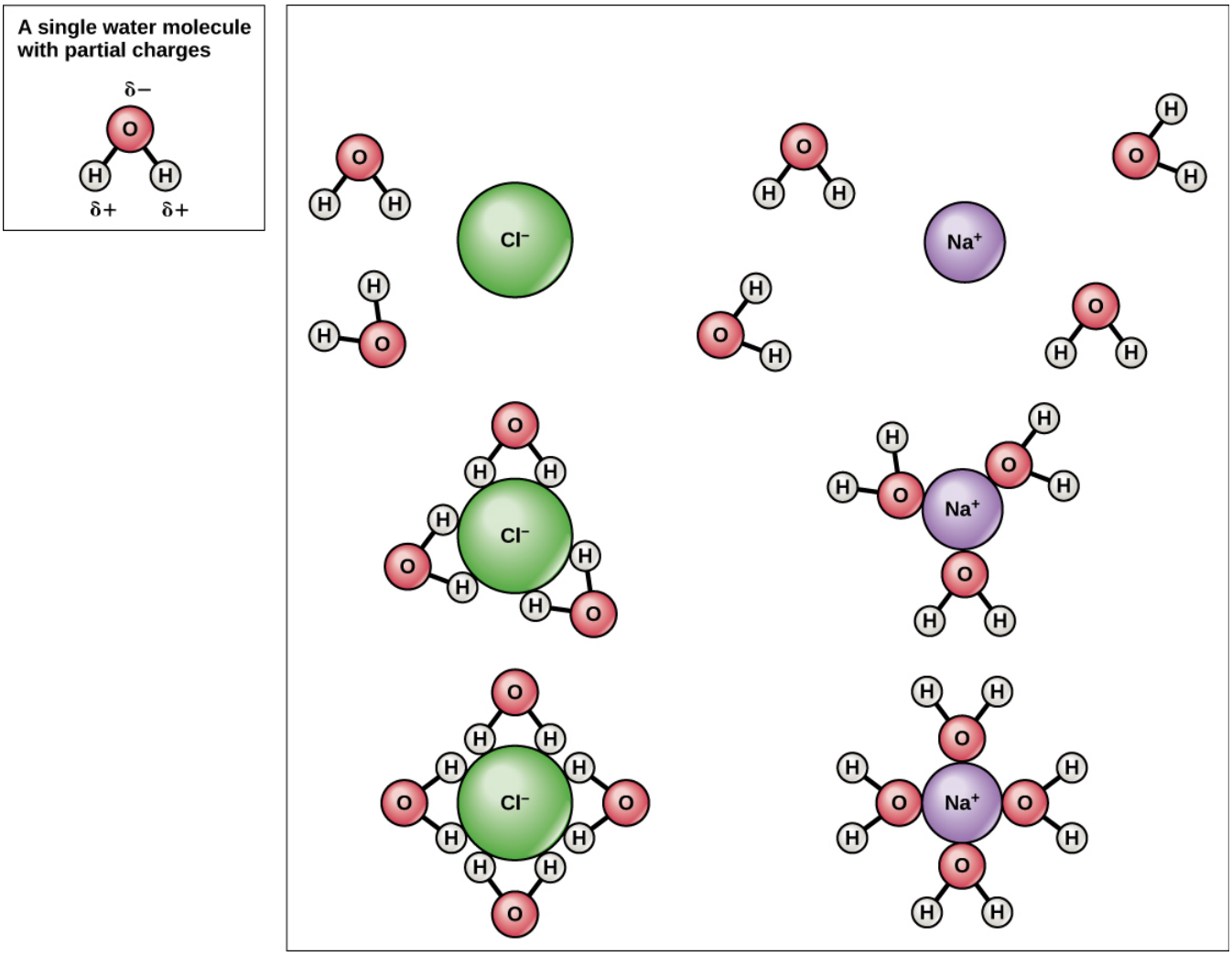


Figure 2.1.3**:** When table salt (NaCl) is mixed in water, spheres of hydration form around the ions.

Water Is Cohesive

Have you ever filled up a glass of water to the very top and then slowly added a few more drops? Before it overflows, the water actually forms a dome-like shape above the rim of the glass. This water can stay above the glass because of the property of cohesion. In cohesion, water molecules are attracted to each other (because of hydrogen bonding), keeping the molecules together at the liquid-air (gas) interface. Cohesion gives rise to surface tension, the capacity of a substance to withstand rupture when placed under tension or stress. When you drop a small scrap of paper onto a droplet of water, the paper floats on top of the water droplet, although the object is denser (heavier) than the water. This occurs because of the surface tension that is created by the water molecules. Cohesion and surface tension keep the water molecules intact and the item floating on the top. It is even possible to "float" a steel needle on top of a glass of water if you place it gently, without breaking the surface tension (Figure 2.1.4).



Figure 2.1.4**:** The weight of a needle on top of water pulls the surface tension downward; at the same time, the surface tension of the water is pulling it up, suspending the needle on the surface of the water and keeping it from sinking. Notice the indentation in the water around the needle (credit: Cory Zanker).

These cohesive forces are also related to the water's property of adhesion, or the attraction between water molecules and other molecules. This is observed when water "climbs" up a straw placed in a glass of water. You will notice that the water appears to be higher on the sides of the straw than in the middle. This is because the water molecules are attracted to the straw and therefore adhere to it.

Cohesive and adhesive forces are important for sustaining life. For example, because of these forces, water can flow up from the roots to the tops of plants for use in photosynthesis. Many aquatic organisms such as water striders or snails can travel along the surface of the water because of surface tension created by cohesive forces.

CONCEPT IN ACTION

To learn more about water, visit the U.S. Geological Survey Water Science for Schools: All About Water! website.

pH, Acids, Bases, and Buffers

The pH of a solution is a measure of its acidity or alkalinity. You have probably used litmus paper, paper that has been treated with a natural water-soluble dye so it can be used as a pH indicator, to test how much acid or base (alkalinity) exists in a solution. You might have even used some to make sure the water in an outdoor swimming pool is properly treated. In both cases, this pH test measures the amount of hydrogen ions that exists in a given solution. High concentrations of hydrogen ions yield a low pH (or acidic), whereas low levels of hydrogen ions result in a high pH (or alkaline/basic). The overall concentration of hydrogen ions is inversely related to its pH and can be measured on the pH scale (Figure 2.1.5). Therefore, the more hydrogen ions present, the lower the pH; conversely, the fewer hydrogen ions, the higher the pH.

The pH scale ranges from 0 to 14. A change of one unit on the pH scale represents a change in the concentration of hydrogen ions by a factor of 10, a change in two units represents a change in the concentration of hydrogen ions by a factor of 100. Thus, small changes in pH represent large changes in the concentrations of hydrogen ions. Pure water is neutral. It is neither acidic nor alkaline, and has a pH of 7.0. Anything below 7.0 (ranging from 0.0 to 6.9) is acidic, and anything above 7.0 (from 7.1 to 14.0) is alkaline. The blood in your veins is slightly alkaline (pH = 7.4). The environment in your stomach is highly acidic (pH = 1 to 2). Orange juice is mildly acidic (pH = approximately 3.5), whereas baking soda is basic (pH = 9.0).

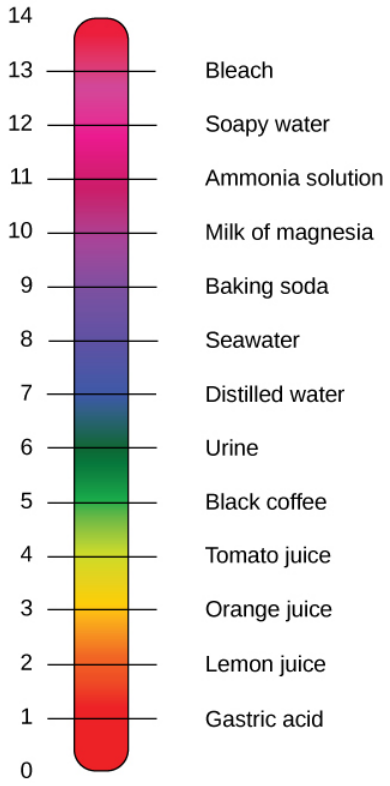


Figure 2.1.5**:** The pH scale measures the amount of hydrogen ions (H^+) in a substance (credit: modification of work by Edward Stevens).

Acids are substances that provide hydrogen ions (H^+) and lower pH, whereas bases provide hydroxide ions (OH^-) and raise pH. The stronger the acid, the more readily it donates H^+. For example, hydrochloric acid and lemon juice are very acidic and readily give up H^+ when added to water. Conversely, bases are those substances that readily donate OH^-. The OH^- ions combine with H^+ to produce water, which raises a substance's pH. Sodium hydroxide and many household cleaners are very alkaline and give up OH^- rapidly when placed in water, thereby raising the pH.

Most cells in our bodies operate within a very narrow window of the pH scale, typically ranging only from 7.2 to 7.6. If the pH of the body is outside of this range, the respiratory system malfunctions, as do other organs in the body. Cells no longer function properly, and proteins will break down. Deviation outside of the pH range can induce coma or even cause death.

So how is it that we can ingest or inhale acidic or basic substances and not die? Buffers are the key. Buffers readily absorb excess H^+ or OH^-, keeping the pH of the body carefully maintained in the aforementioned narrow range. Carbon dioxide is part of a prominent buffer system in the human body; it keeps the pH within the proper range. This buffer system involves carbonic acid (H_2CO_3) and bicarbonate (HCO_3^-) anion. If too much H^+ enters the body, bicarbonate will combine with the H^+ to create carbonic acid and limit the decrease in pH. Likewise, if too much OH^- is introduced into the system, carbonic acid will rapidly dissociate into bicarbonate and H^+ ions. The H^+ ions can combine with the OH^- ions, limiting the increase in pH. While carbonic acid is an important product in this reaction, its presence is fleeting because the carbonic acid is released from the body as carbon dioxide gas each time we breathe. Without this buffer system, the pH in our bodies would fluctuate too much and we would fail to survive.

The same buffer system also works in the ocean where CO_2 reacts with seawater to form carbonic acid (H_2CO_3), which dissociates into bicarbonate (HCO_3^-) and carbonate (CO_3^{2-}) ions:

$$CO_2 + H_2O \Leftrightarrow H_2CO_3 \Leftrightarrow HCO_3^- + H^+ \Leftrightarrow CO_3^{2-} + 2H^+ \tag{2.1.1}$$

The sum of these three carbon species is called dissolved inorganic carbon ($DIC = CO_2 + HCO_3^- + CO_3^{2-}$) or total carbon. The equilibrium between the species depends on the pH. In the current ocean, pH is about 8.1, which leads to about 86.5 % of DIC being in the form of bicarbonate ions, 13.0 % in the form of carbonate ions, and only 0.5 % in the form of aqueous CO_2 (Fig. \(\PageIndex{6}; Zeebe and Wolf-Gladrow, 2001).

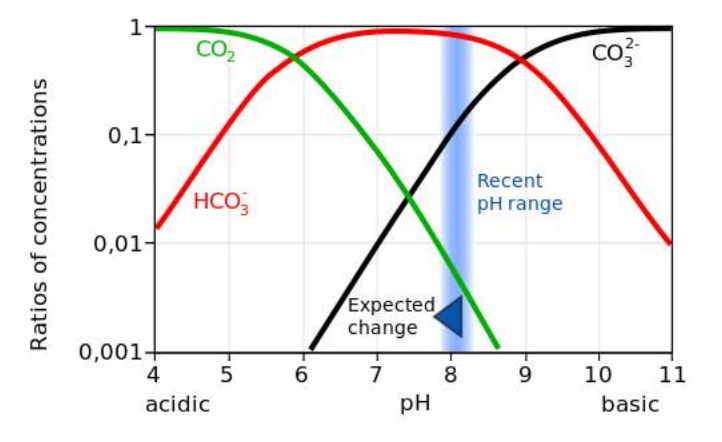


Figure 2.1.6**:** Ratios of carbonate species concentrations as a function of the pH. Currently average seawater has a pH of about 8.1. Therefore most carbon in the ocean is in the form of bicarbonate. Addition of anthropogenic CO_2 decreases the pH. "Bjerrum Plot" is available in the public domain.

Dissociation of carbonic acid into bicarbonate (baking soda) produces a hydrogen ion H^+, which increases the pH of the water. Most hydrogen ions, however, re-combine with carbonate ions to form additional bicarbonate ions. Nevertheless, adding CO_2 to seawater increases its hydrogen ion concentration (decreases its pH) and decreases the carbonate ion concentration. This process is called ocean acidification.

Summary

Water has many properties that are critical to maintaining life. It is a polar molecule, allowing for the formation of hydrogen bonds, which allow ions and other polar molecules to dissolve in water. Therefore, water is an excellent solvent. The hydrogen bonds between water molecules give water the ability to hold heat better than many other substances. As the temperature rises, the hydrogen bonds between water continually break and reform, allowing for the overall temperature to remain stable, although increased energy is added to the system. Water's cohesive forces allow for the property of surface tension. All of these unique properties of water are important in the chemistry and physics of living organisms.

The pH of a solution is a measure of the concentration of hydrogen ions in the solution. A solution with a high number of hydrogen ions is acidic and has a low pH value. A solution with a high number of hydroxide ions is basic and has a high pH value. The pH scale ranges from 0 to 14, with a pH of 7 being neutral. Buffers are solutions that moderate pH changes when an acid or base is added to the buffer system. Buffers are important in biological systems because of their ability to maintain constant pH conditions.

Sources

Humphrey, W., Dalke, A., & Schulten, K. (1996). VMD—Visual Molecular Dynamics. *Journal of Molecular Graphics*, *14*(1), 33–38. http://www.ks.uiuc.edu/Research/vmd/

Zeebe, R. E., & Wolf-Gladrow, D. A. (2001). *CO_2 in seawater: Equilibrium, kinetics, isotopes*. Elsevier.

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- 2.1: The Building Blocks of Molecules https://bio.libretexts.org/Bookshelv...fig-ch02_01_06
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2.2: Water (Hydrologic) Cycle

Water is essential for all living processes. The human body is more than one-half water and human cells are more than 70 percent water. Water is also the only substance that occurs naturally on earth in three forms: solid, liquid and gas. Of the stores of water on Earth, 97.5% is salt water (Figure 2.2.1). Of the remaining water, 99% is locked as underground water or ice. Ice caps and glaciers are the largest reservoirs of fresh water but this water is inconveniently located, mostly in Antarctica and Greenland. Shallow groundwater is the largest reservoir of usable fresh water. Less than one percent of fresh water is present in lakes and rivers, the most heavily used water resource.

Many organisms are dependent on this small amount of surface fresh water supply, a lack of which can have important effects on ecosystem dynamics. If all of world's water was shrunk to the size of 1 gallon, then the total amount of fresh water would be about 1/3 cup, and the amount of readily usable fresh water would be 2 tablespoons.

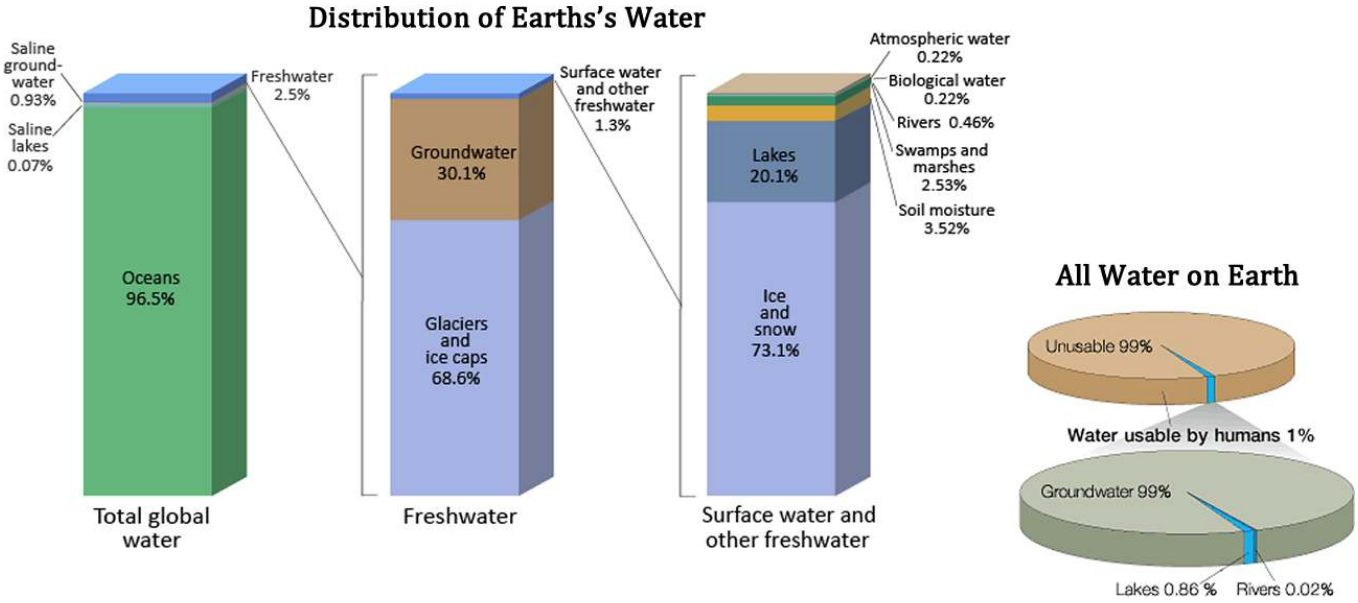


Figure 2.2.1**: Earth's Water Reservoirs** -- Bar chart Distribution of Earth's water including total global water, fresh water, and surface water and other fresh water and Pie chart Water usable by humans and sources of usable water. *Source: United States Geographical Survey Igor Skiklomanov's chapter "World fresh water resources" in Peter H. Gleick (editor), 1993, Water in Crisis: A Guide to the World's Fresh Water Resources.*

Water Reservoirs

The **hydrosphere** is the area of Earth where water movement and water storage occurs. **Water reservoirs** are the locations where water is stored. (Note that this term can also refer to artificial lakes created by dams.) Water is found as a liquid on the surface (rivers, lakes, oceans) and beneath the surface (groundwater), as ice (polar ice caps and glaciers), and as water vapor in the atmosphere. Figure 2.2.2 illustrates the average time that an individual water molecule may spend in the Earth's major water reservoirs. **Residence time** is a measure of the average time an individual water molecule stays in a particular reservoir.

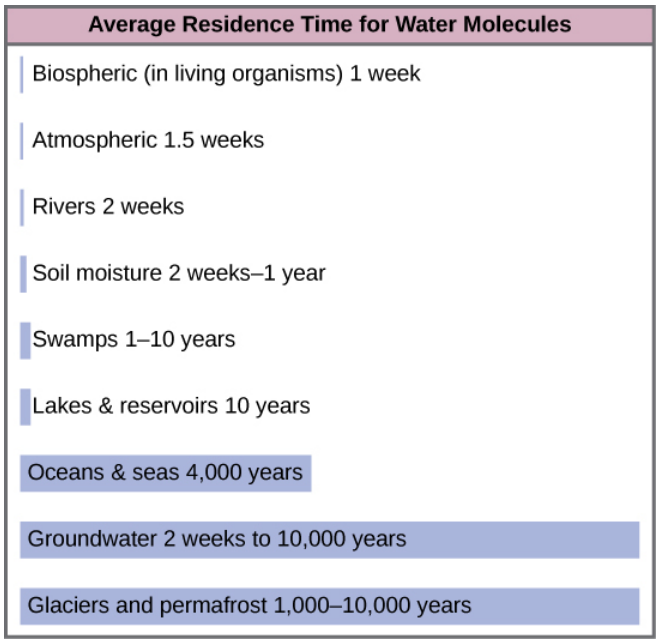


Figure 2.2.2**:** Average residence time that water remains in each reservoir. Image from OpenStax is licensed under CC-BY.

The Water Cycle

The various processes that occur during the cycling of water are illustrated in Figure 2.2.3. The processes include the following:

- evaporation and sublimation
- transpiration
- condensation and precipitation
- infiltration and subsurface water flow (groundwater discharge)
- surface runoff and snowmelt
- streamflow

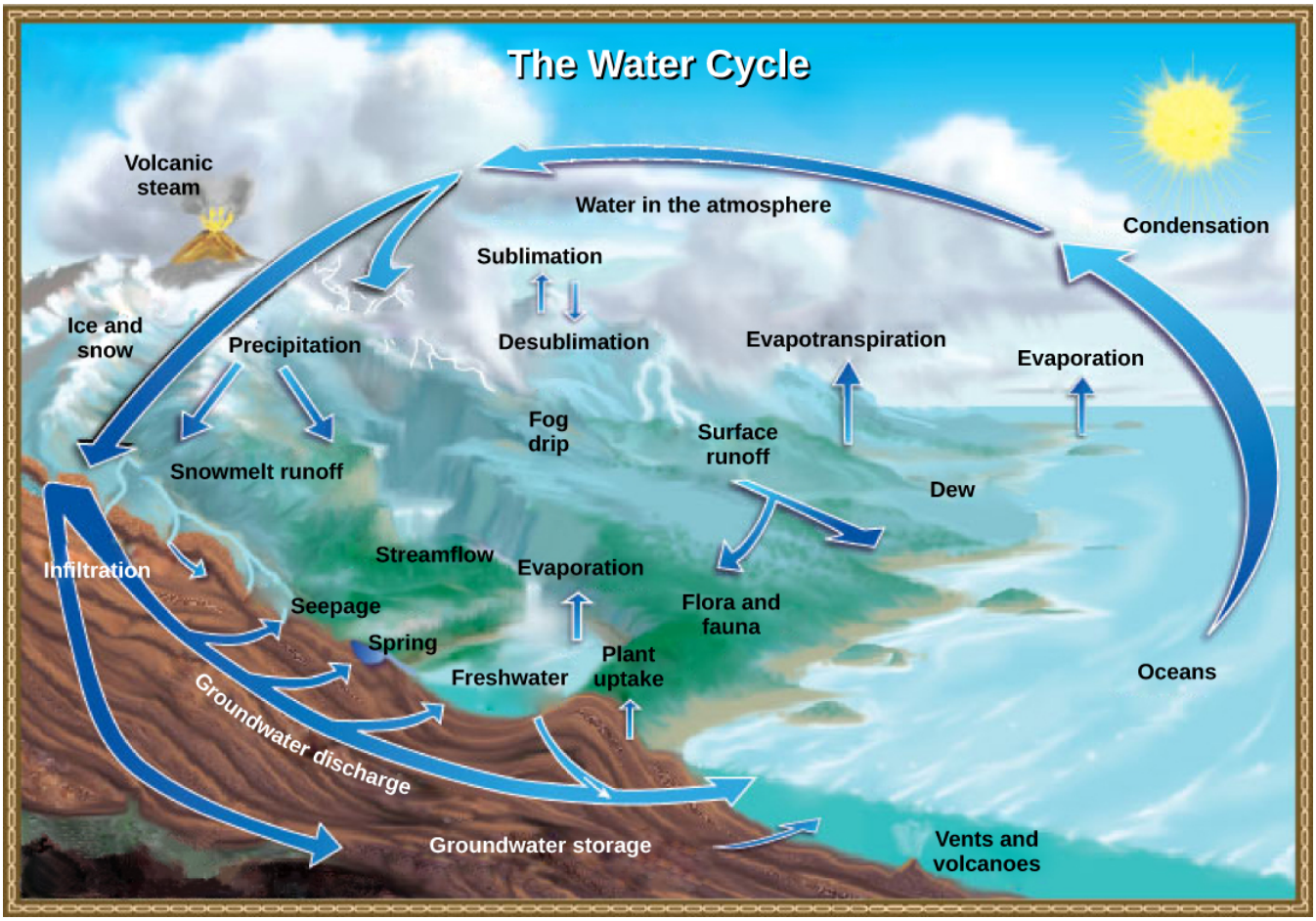


Figure 2.2.3**:** Water from the land and oceans enters the atmosphere by evaporation or sublimation, where it condenses into clouds and falls as rain or snow. Precipitated water may enter freshwater bodies or infiltrate the soil. The cycle is complete when surface or groundwater reenters the ocean (credit: modification of work by John M. Evans and Howard Perlman, USGS).

The water cycle is driven by the Sun's energy as it warms the oceans and other surface waters. This leads to evaporation (water to water vapor) of liquid surface water and sublimation (ice to water vapor) of frozen water, thus moving large amounts of water into the atmosphere as water vapor. As the water vapor rises in the atmosphere, it cools and condenses. **Condensation** is the process in which water vapor changes to tiny droplets of liquid water. Over time, this water vapor condenses into clouds as liquid or frozen droplets and eventually leads to precipitation (rain or snow), which returns water to Earth's surface. Most precipitation falls into the ocean. Some frozen precipitation becomes part of ice caps and glaciers. These masses of ice can store frozen water for hundreds of years or longer. Rain reaching Earth's surface may evaporate again, flow over the surface, or percolate into the ground. Most easily observed is surface runoff: the flow of fresh water either from rain or melting ice. Runoff can make its way through streams and lakes to the oceans or flow directly to the oceans themselves.

In most natural terrestrial environments rain encounters vegetation before it reaches the soil surface. A significant percentage of water evaporates immediately from the surfaces of plants. What is left reaches the soil and begins to move down. Surface runoff will occur only if the soil becomes saturated with water in a heavy rainfall. **Infiltration** is the process through which water sinks into the ground and is determined by the soil or rock type through which water moves. Soil texture (particle size) is an important control on water movement. Most water in the soil will be taken up by plant roots. Water enters the vascular system of the plant through the roots and evaporates, or transpires, through the stomata of the leaves. The plant will use some of this water for its own metabolism, and some of that will find its way into animals that eat the plants, but much of it will be lost back to the atmosphere through a process known as **evapotranspiration**. Water in the soil that is not taken up by a plant and that does not evaporate is able to percolate into the subsoil and bedrock. Here it forms groundwater.

Groundwater is a significant reservoir of fresh water. It exists in the pore spaces between particles in sand and gravel, or in the fissures in rocks. Shallow groundwater flows slowly through these pore spaces and fissures and eventually finds its way to a stream or lake where it becomes a part of the surface water again. Streams do not flow because they are replenished from rainwater directly; they flow because there is a constant inflow from groundwater below. Some groundwater is found very deep in the bedrock and can persist there for millennia. Most groundwater reservoirs, or **aquifers**, are the source of drinking or irrigation water drawn up through wells. In many cases these aquifers are being depleted faster than they are being replenished by water percolating down from above.

An important part of the water cycle is how water varies in salinity, which is the abundance of dissolved ions in water. Freshwater (such as lakes, rivers, and near-surface groundwater) has a relatively low salinity. The saltwater in the oceans is highly saline, with about 35,000 mg of dissolved ions per liter of seawater. Evaporation is a distillation process that produces nearly pure water with almost no dissolved ions. As water vaporizes, it leaves the dissolved ions in the original liquid phase. Eventually, condensation forms clouds and sometimes precipitation. After rainwater falls onto land, it dissolves minerals in rock and soil, which increases its salinity. Rain and surface runoff are major ways in which minerals, including phosphorus and sulfur, are cycled from land to water.

Precipitation Patterns

Rain and surface runoff are major ways in which minerals, including carbon, nitrogen, phosphorus, and sulfur, are cycled from land to water. More precipitation falls near the equator, and landmasses there are characterized by a tropical rainforest climate (Figure 2.2.4). Less precipitation tends to fall near 20–30° north and south latitude, where the world's largest deserts are located. These rainfall and climate patterns are related to global wind circulation cells. The intense sunlight at the equator heats air, causing it to rise and cool, which decreases the ability of the air mass to hold water vapor and results in frequent rainstorms. Around 30° north and south latitude, descending air conditions produce warmer air, which increases its ability to hold water vapor and results in dry conditions. Both the dry air conditions and the warm temperatures of these latitude belts favor evaporation. Global precipitation and climate patterns are also affected by the size of continents, major ocean currents, and mountains.

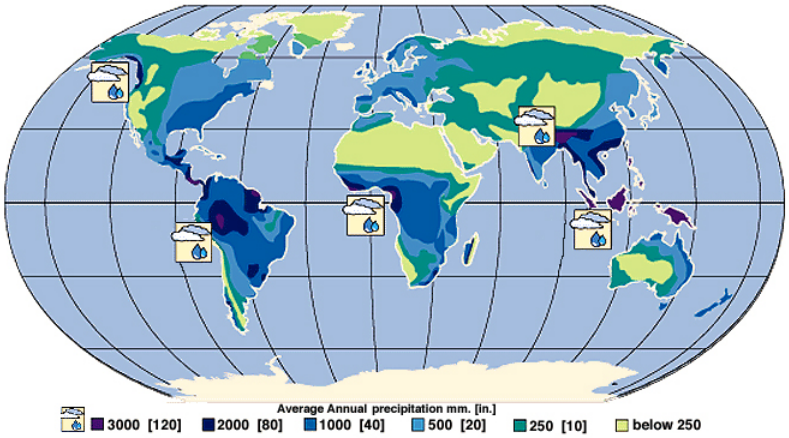


Figure 2.2.4: World Rainfall Map -- The false-color map above shows the amount of rain that falls around the world. Areas of high rainfall include Central and South America, western Africa, and Southeast Asia. Since these areas receive so much rainfall, they are where most of the world's rainforests grow. Areas with very little rainfall usually turn into deserts. The desert areas include North Africa, the Middle East, western North America, and Central Asia. *Source: United States Geological Survey Earth Forum, Houston Museum Natural Science.*

In the United States, the 100th Meridian roughly marks the boundary between the humid and arid parts of the country (figure 2.2.5). Irrigation is required to grow crops west of the 100th Meridian. In the West, surface water is stored in reservoirs (artificial lakes) and mountain snowpacks and strategically released through a system of canals during times of high use.

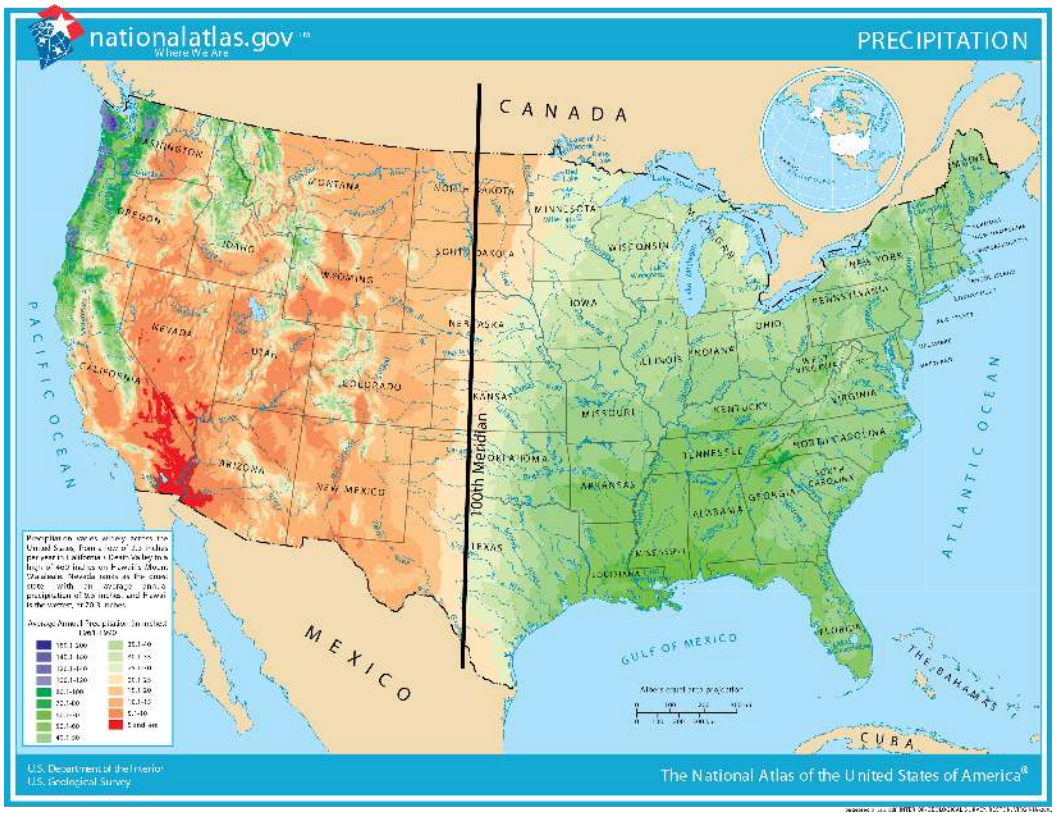
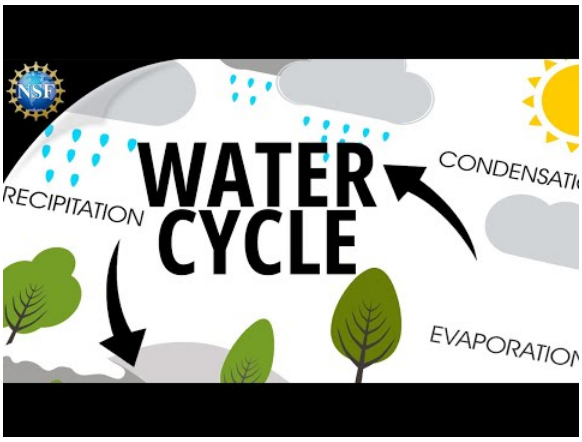


Figure 2.2.5**:** Distribution of precipitation in the United States. The 100th Meridian is approximately where the average precipitation transitions from relatively wet to dry. Eastern states are mostly green, indicating greater precipitation than most western states, which are mainly orange or red (indicating low precipitation). *Source: U.S. Geological Survey.*

Further "Reading"

The steps of the water cycle are also explained in the video below.





For more information on the water cycle you might want to watch this water cycle video from USGS.

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2.3: Soils

Soil is the outer loose layer that covers the surface of Earth. Soil quality is a major determinant, along with climate, of plant distribution and growth. Soil quality depends not only on the chemical composition and texture of the soil, but also the topography (regional surface features) and the presence of living organisms. In agriculture, the history of the soil, such as the cultivating practices and previous crops, modify the characteristics and fertility of that soil.

Soil develops very slowly over long periods of time, and its formation results from natural and environmental forces acting on mineral, rock, and organic compounds. Soils can be divided into two groups: organic soils are those that are formed from sedimentation and primarily composed of organic matter, while those that are formed from the weathering of rocks and are primarily composed of inorganic material are called mineral soils. Mineral soils are predominant in terrestrial ecosystems, where soils may be covered by water for part of the year or exposed to the atmosphere.

Soil is Important

Soil is important to our society primarily because it provides the foundation of agriculture and forestry. Soil plays a key role in plant growth. Beneficial aspects to plants include providing physical support, water, heat, nutrients, and oxygen. Mineral nutrients from the soil can dissolve in water and then become available to plants. Soil plays a role in nearly all biogeochemical cycles on the Earth's surface. Global cycling of key elements such as carbon (C), nitrogen (N), phosphorous (P), and sulfur (S) all pass through soil. In the hydrologic (water) cycle, soil helps to mediate **infiltration** (percolating) from the surface into the groundwater. Microorganisms living in soil can also be important components of biogeochemical cycles through the action of decomposition and other processes such as nitrogen fixation.

Through their roots, plants absorb water and minerals (e.g., nitrates, phosphates, potassium, copper, zinc). Of the mineral nutrients absorbed from the soil, **macronutrients**, including nitrogen (N), potassium (K), calcium (Ca), magnesium (Mg), phosphorus (P), sulfur (S), and silicon (Si) are needed by plants in significant quantities. **Micronutrients** are essential elements that are needed only in small quantities, but can still be limiting to plant growth since these nutrients are not so abundant in nature. Micronutrients include chlorine (Cl), iron (Fe), boron (B), manganese (Mn), sodium (Na), zinc (Zn), copper (Cu), nickel (Ni), and molybdenum (Mo). There are some other elements that tend to aid plant growth but are not absolutely essential.

Micronutrients and macronutrients are desirable in particular concentrations and can be detrimental to plant growth when concentrations in soil solution are either too low (limiting) or too high (toxicity). Mineral nutrients are useful to plants only if they are in an extractable form in soil solutions, such as a dissolved ion rather than in solid mineral. Many nutrients move through the soil and into the root system as a result of concentration gradients, moving by diffusion from high to low concentrations across semi-permeable membranes in root cells (passive transport). However, some nutrients are selectively absorbed by active transport across the root membranes, enabling concentrations to become higher inside the plant than in the soil.

Although many aspects of soil are beneficial to plants, excessively high levels of trace metals (either naturally occurring or added by humans) or applied herbicides can be toxic to some plants (Figure 2.3.1).



Figure 2.3.1**:** These native plants are affected by herbicides that were used to kill nearby weeds. Image by Matt Lavin is available under CC-BY-SA 2.0.

An important factor affecting soil fertility is soil **pH** (the negative log of the hydrogen ion concentration). Soil pH is a measure of the acidity or alkalinity of the soil solution. On the pH scale (0 to 14) a value of seven represents a neutral solution; a value less than seven represents an **acidic** solution and a value greater than seven represents an **alkaline** solution. Soil pH affects the health of microorganisms in the soil and controls the availability of nutrients in the soil solution. Strongly acidic soils (less than 5.5) hinder the growth of bacteria that decompose organic matter in the soil. This results in a buildup of organic matter that has yet to be decomposed, which leaves important nutrients such as nitrogen in forms that are unusable by plants. Soil pH also affects the solubility of nutrient-bearing minerals. This is important because the nutrients must be dissolved in solution for plants to assimilate them through their roots. Most minerals are more soluble in slightly acidic soils than in neutral or slightly alkaline soils. Strongly acid soils (pH four to five), though, can result in high concentrations of aluminum, iron and manganese in the soil solution, which may inhibit the growth of some plants.

Several factors determine soil pH. Organic material in soil decreases pH to an extent, but it also acts as a **buffer**, limiting changes in pH. Climate is also important, with high amounts of rainfall lowering pH and increasing leaching (draining of nutrients and other dissolved ions with percolating water). Some types of parent material, such as those high in silicon, decrease pH, while others, such as limestone increase pH.

Soil Composition

Soil consists of organic matter (about 5%), inorganic mineral matter (40-45% of soil volume), water (about 25%) and air (about 25%) (Figure 2.3.2). The amount of each of the four major components of soil depends on the amount of vegetation, soil compaction, and water present in the soil.

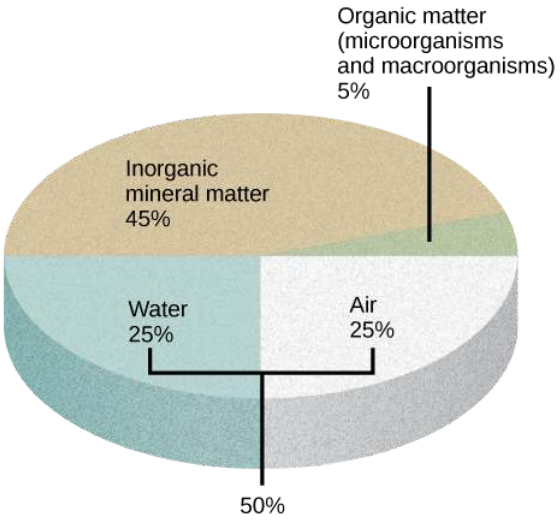


Figure 2.3.2**:** The four major components of soil are shown: inorganic minerals, organic matter, water, and air. Image is from OERTX and is available in the public domain.

The organic material consists of dead organisms in various stages of decomposition. It is dark-colored because it contains **humus**, partially decayed matter containing organic acids. Humus enriches the soil with nutrients, gives the soil a loose texture that holds water, and allows air to diffuse through it. Oxygen is important for plant roots and many inhabitants of the soil. The organic component of soil serves as a cementing agent, returns nutrients to the plant, allows soil to store moisture, makes soil tillable for farming, and provides energy for soil microorganisms. Most soil microorganisms—bacteria, algae, or fungi—are dormant in dry soil, but become active once moisture is available.

The inorganic material of soil consists of rock, slowly broken down into smaller particles that vary in size. Soil particles that are 100 µm to 2 mm in diameter are **sand**. (A **micrometer**, µm, 10^{-6} m, or a millionth of a meter.) Soil particles between 2 and 100 µm are called **silt**, and even smaller particles, less than 2 µm in diameter, are called **clay**.

Soil should ideally contain 50 percent solid material and 50 percent pore space (Figure 2.3.3). **Pore space** refers to the gaps in between soil particles. The larger the soil particles, the larger the pore spaces. Water can quickly pass through large pore spaces, so soils high in sand drain easily. Smaller soil particles have more surface area relative to volume and produce narrow pore spaces. Water clings to these surfaces, and soils high in clay thus retain water. (Clay is also negatively charged, which attracts water.) About one-half of the pore space should contain water, and the other half should contain air.

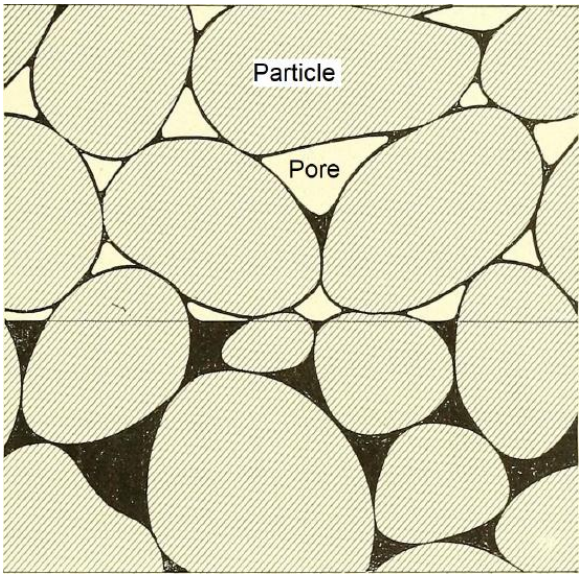


Figure 2.3.3**:** Soil particles and the pore spaces in between them. The black shading represents water, which fills the pore spaces in the lower portion of the soil and clings to narrow portions of pore space in the top portion of the soil. Image from "Forest physiography; physiography of the United States and principles of soils in relation to forestry" is available in the public domain.

Soil texture is based on percentages of sand, silt, and clay (Figure 2.3.4). Soils that have a high percentage of one particle size are named after that particle (a clay soil has a high percentage of clay). Other soils have a mixture of two particle sizes and very little of the third size. For example, silty clay has roughly 50% clay and 50% silt while sandy clay has 50-60% sand and 35-50% clay. Some soils have no dominant particle size and contain a mixture of sand, silt, and humus. These soils are called **loams**, and they are optimal for agriculture. A medium loam has roughly 40% sand, 40% silt, and 20% clay. Larger particles (sand) facilitate drainage, and small particles (clay) facilitate water retention, so loam soils both have good drainage and can remain moist. Soils that deviate slightly from a medium loam include loamy sand, sandy loam, sandy clay loam, clay loam, silty clay loam, and silty loam.

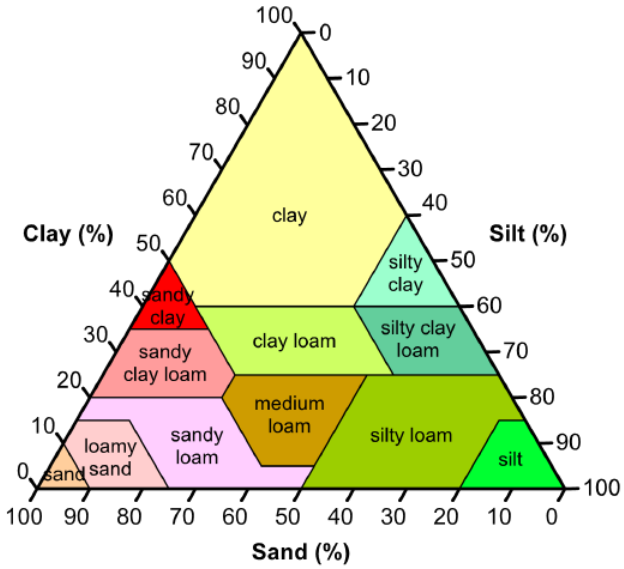


Figure 2.3.4**:** A soil texture triangle is used to determine the soil texture based on the percentages of sand, silt, and clay. The left axis represents the percentage of clay. The right axis represents the percentage of silt. The bottom axis represents the percentage of sand. Most soils that contain more than 40% of clay particles are classified as clays. Exceptions are silty clays, which contain 40-60% clay and 40-60% silt. Another exception are sandy clays, which contain 35-50% clay and 50-70% sand. Clay loams and silty clay loams contain 25-40% clay. Clay loams contain 20-60% silt, and silty clay loams contain 60-75% silt. Sandy clay loams contain 20-35% clay and 50-80% sand. Medium loams contain 5-25% clay, 20-50% silt, and 30-55% sand. Soils with more than 50% silt and no more than 25% clay are either silty loams or silts. Silts have 80-100% silt and no more than 15% clay. Sand have 90-100% sand. Loamy sands have 75-90% sand and no more than 15% clay. A soil with a composition that does not fit into the already described categories would be a sandy loam. To determine the soil texture, first find the percentage of clay and trace a line horizontally to the right. At the same time, find the percentage of silt and trace a line diagonally (down and to the left, parallel to the clay axis). The two lines will meet at the correct soil type. For example, traced lines from 20% clay and 40% silt intersect at the medium loam category. To confirm, trace a diagonal line (down and to the right, parallel to the sit axis) from this point to the sand axis. This line cross the axis at 40%. In summary, a line can be traced from each axis that is parallel to axis that is counterclockwise of it. "Soil Composition" by Richard Wheeler is available under CC-BY-SA 3.0.

Soils can be divided into two groups based on how they form. **Organic soils** are those that are formed from sedimentation and often contain more than 30% organic matter. They form when organic matter, such as leaf litter, is deposited more quickly than it can be decomposed (Figure 2.3.5). **Mineral soils** are formed from the weathering of rocks, typically contain no more than 30% organic matter, and are primarily composed of inorganic material. **Weathering** occurs when biological, physical, and chemical processes, such as erosion, leaching, or high temperatures, break down rocks.



Figure 2.3.5**:** Decomposition of organic material occurs very slowly in this acidic bog. The organic material accumulates, which is characteristic of organic soils. "Sphagnum Bog" by William L. Farr is available under CC-BY-SA 4.0.

Soil has Horizons

Soil distribution is not uniform because its formation results in the production of layers; together, the vertical section of a soil is called the **soil profile**. Within the soil profile, soil scientists define zones called horizons. A **horizon** is a soil layer with distinct physical and chemical properties that differ from those of other layers.

The soil profile has four distinct layers: 1) O horizon; 2) A horizon; 3) B horizon and 4) C horizon (Figure 2.3.6).

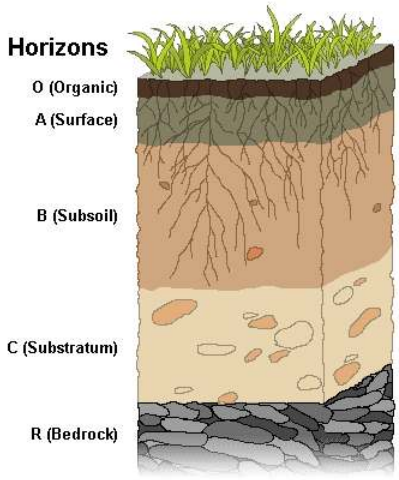


Figure 2.3.6**:** This image shows the different horizons, or layers, in soil. Vegetation grows at the surface. The top, deep brown layer is the O (organic) horizon. Below this is the gray A horizon (topsoil, or surface). Next is the light brown B horizon (subsoil). The C horizon (substratum, or soil base) is tan and includes larger pieces of rocks. The gray bedrock is the deepest layer. The E (eluviated) horizon that is sometimes found between the A and B horizons is absent here. "Graphic of Soil Profile" by Wilsonbiggs is licensed under CC BY-SA 4.0.

Upper horizons (labeled as the A and O horizons) are richer in organic material and so are important in plant growth, while deeper layers (such as the B and C horizons) retain more of the original features of the bedrock below. Some soils may have additional layers (like the E horizon, Figure 2.3.7), or lack one of these layers. The thickness of the layers is also variable, and depends on the factors that influence soil formation. In general, immature soils may have O, A, and C horizons, whereas mature soils may display all of these, plus additional layers.

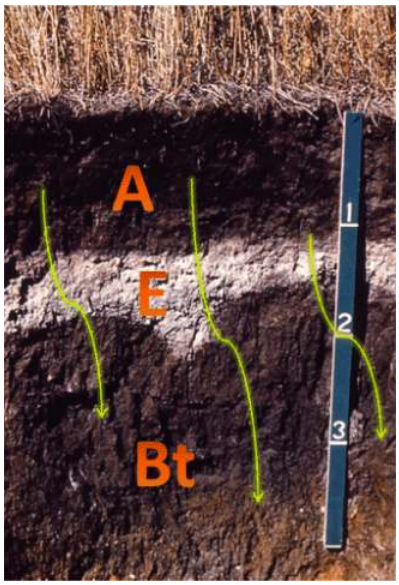


**Figure 2.3.7): ** Photograph shows a soil profile from South Dakota revealing three horizons. The A horizon (topsoil) is dark brown and extend about 1 foot. Below it is the white E (eluviated) horizon, which is about 6 inches thick. The B horizon (subsoil, labeled Bt) is the medium brown and the lowest visible layer The yellow arrows symbolize translocation of fine clays to the B horizon. The scale is in feet. *Source: University of Idaho and modified by D. Grimley*.

O horizon

The very top of the **O horizon** consists of partially decayed organic debris like leaves (Figure 2.3.6). This horizon is usually dark in color because of humus.

A horizon

The **A horizon** (topsoil) consists of a mixture of organic material (from decomposition) with inorganic products of chemical weathering of rocks, and it is therefore the beginning of true mineral soil (Figure 2.3.7). In this area, rainwater percolates through the soil and carries materials from the surface. The A horizon may be only 5 cm (2 in.), or it may over a meter. For instance, river deltas like the Mississippi River delta have deep layers of topsoil. Microbial processes occur in the top soil, and this horizon supports plant growth. Many organisms, such as earthworms and insects live among the plant roots in this horizon.

B horizon

The **B horizon** (subsoil) consists of small particles that have moved downward, resulting in a dense layer in the soil (Figure 2.3.7). In some soils, the B horizon contains nodules or a layer of calcium carbonate. The subsoil is usually lighter in color than topsoil and often contains an accumulation of minerals.

C horizon

The **C horizon** (soil base), includes the **parent material**, the organic and inorganic substances from which soils form (Figure 2.3.6). Weathering parent material represents the first steps in the chemical breakdown of rock into soil. Often the weathered parent material is underlain by the parent material itself, although in some places it has been carried from another location by wind, water, or glaciers. Beneath the C horizon lies bedrock. The chemical nature of the parent material, whether granite, limestone, or sandstone, for example, has a great influence on the fertility of the soil derived from it.

Several Factors Affect Soil Formation and Composition

The fundamental factors that affect soil genesis can be categorized into five elements: climate, organisms, topography, parent material, and time. One could say that the relief, climate, and organisms dictate the local soil environment and act together to cause weathering and mixing of the soil parent material over time.

Climate

The role of climate in soil development includes aspects of temperature and precipitation. Soils in very cold areas with permafrost conditions (such as the arctic tundra) tend to be shallow and weakly developed due to the short growing season. In warm, tropical climates, soils tend to be thicker (but lacking in organic matter), with extensive leaching and mineral alteration. In such climates, organic matter decomposition and chemical weathering occur at an accelerated rate. The presence of moisture and nutrients from weathering will also promote biological activity: a key component of a quality soil.

Ancient soils, sometimes buried and preserved in the subsurface, are referred to as **paleosols** (Figure 2.3.8) and reflect past climatic and environmental conditions.

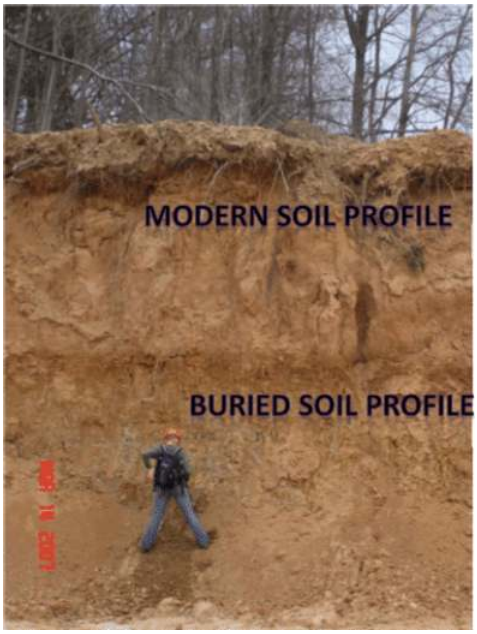


Figure 2.3.8**:** Modern versus Buried Soil Profiles: a buried soil profile, or paleosol (above geologist ‘s head), represents soil development during the last interglacial period, while a modern soil profile (Alfisol) occurs near the land surface. *Source: D. Grimley*.

Organisms

The presence of living organisms in the soil (**soil biota**) greatly affects soil formation and structure. A diversity of animals are found in the soil such as nematodes, spiders, insects, centipedes, millipedes, pillbugs, slugs, and earthworms (Figure 2.3.9). The soil also contains microorganisms like bacteria, archaea, fungi, and "protists". Animals and microorganisms can produce pores and crevices, and plant roots can penetrate into crevices to produce more fragmentation. Additionally, leaves and other material that fall from plants decompose and contribute to soil composition. Microorganisms not only decompose organic matter, but contribute to other processes in nutrient cycles, such as nitrogen fixation. Many soil animals also contribute decomposition either directly as detritivores or indirectly through the soil food web.

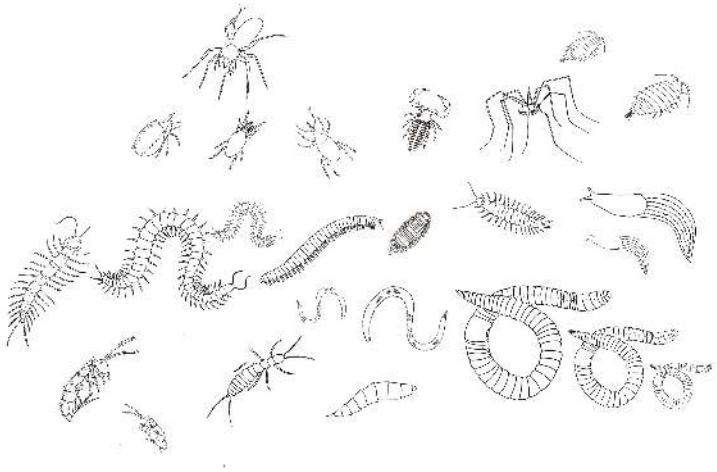


Figure 2.3.9**:** Illustration of animals commonly found in the soil. "Soil Fauna" by Arne Henriks is licensed under CC BY 2.0.

Parent Material

Mineral soils form directly from the weathering of bedrock, the solid rock that lies beneath the soil, and therefore, they have a similar composition to the original rock. Other soils form in materials that came from elsewhere, such as sand and glacial drift. Materials located in the depth of the soil are relatively unchanged compared with the deposited material. Sediments in rivers may have different characteristics, depending on whether the stream moves quickly or slowly. A fast-moving river could have sediments of rocks and sand, whereas a slow-moving river could have fine-textured material, such as clay.

The type of parent material may also affect the rapidity of soil development. Parent materials that are highly weatherable (such as volcanic ash) will transform more quickly into highly developed soils, whereas parent materials that are quartz-rich rocks (and more difficult to break down) will take longer to develop into soils. Parent materials also provide nutrients to plants and can affect soil internal drainage.

Topography

Regional surface features (familiarly called “the lay of the land”) can have a major influence on the characteristics and fertility of a soil. Topography affects water runoff, which strips away parent material and affects plant growth. Soils on steep slopes are more prone to erosion and may be thinner than soils that are on relatively level ground. **Infiltration**, the percolating of water through the soil, is limited in steep soils.

The local topography can have important microclimatic effects. In the northern hemisphere, south-facing slopes are exposed to more direct sunlight angles and are thus warmer and drier than north-facing slopes. The cooler, moister north-facing slopes have a more dynamic plant community and thicker soils because extensive root systems stabilize the soil and reduce erosion (figure 2.3.10).



Figure 2.3.10**:** A north-facing slope (left) and south-facing slope (right) in the Mediterranean climate (chaparral) of the Santa Monica Mountains, California. Vegetation on the north-facing slope is denser due to cool, moist conditions relative to the south-facing slope. "Slope Effect" by Noah Elhardt is licensed under CC BY-SA 2.5.

Time

Time is an important factor in soil formation because soils develop over long periods. Soil formation is a dynamic process. Materials are deposited over time, decompose, and transform into other materials that can be used by living organisms or deposited onto the surface of the soil.

In general, soil profiles tend to become thicker (deeper), more developed, and more altered over time. However, the rate of change is greater for soils in youthful stages of development. The degree of soil alteration and deepening slows with time and at some point, after tens or hundreds of thousands of years, may approach an equilibrium condition where erosion and deepening (removals and additions) become balanced. **Young soils** (< 10,000 years old) are strongly influenced by parent material and typically develop horizons and character rapidly. Over time, as weathering processes deepen, mix, and alter the soil, the parent material becomes less recognizable as chemical, physical, and biological processes take effect. **Moderate age soils** (roughly 10,000 to 500,000 years old) are slowing in profile development and deepening, and may begin to approach equilibrium conditions. **Old soils** (>500,000 years old) have generally reached their limit as far as soil horizonation and physical structure, but may continue to alter chemically or mineralogically.

Soil development is not always continual. Geologic events such as landslides, glacier advance, or the rising of shorelines can rapidly bury soils. Erosion in rivers and shorelines can cause removal or truncation of soils, and wind or flooding slowly deposit sediment that adds to the soil. Animals can mix the soil and sometimes cause **soil regression**, a reversal or "bump in the road" for the normal path of development, and this increases development over time.

Soil are Classified Into Groups

Soils are classified into one of 12 soil orders based on soil horizons, how they form, and their chemical compositions. For example, Mollisols (Figure 2.3.12), which are found in temperate grasslands, have a thick topsoil rich in organic content. Aridisols, on the other hand, are dry soils that contain calcium carbonate and are found in deserts. Each soil order is further divided into suborders. See USDA's The Twelve Orders of Soil Taxonomy and The Twelve Soil Orders from the University of Idaho for more details.

Contributiors and Attributions

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2.4: The Atmosphere

The Atmosphere

The **atmosphere**, the gaseous layer that surrounds the earth, formed over four billion years ago and is held in place by the attractive forces of gravity. During the evolution of the solid earth, volcanic eruptions released gases into the developing atmosphere. Assuming the outgasing was similar to that of modern volcanoes, the gases released included: water vapor (H_2O), carbon monoxide (CO), carbon dioxide (CO_2), hydrochloric acid (HCl), methane (CH4), ammonia (NH_3), nitrogen (N_2) and sulfur gases. The atmosphere was reducing because there was no free oxygen. Most of the hydrogen and helium that outgassed would have eventually escaped into outer space due to the inability of the earth's gravity to hold on to their small masses. There may have also been significant contributions of volatiles from the massive meteoritic bombardments known to have occurred early in the earth's history.

Water vapor in the atmosphere condensed and rained down, eventually forming lakes and oceans. The oceans provided homes for the earliest organisms which were probably similar to cyanobacteria. Oxygen was released into the atmosphere by these early organisms, and carbon became sequestered in sedimentary rocks. This led to our current oxidizing atmosphere, which is mostly comprised of nitrogen (roughly 78 percent) and oxygen (roughly 21 percent) with 0.9% argon (Ar) and 0.04% carbon dioxide (CO_2). The atmosphere also contains highly variable concentrations of water vapor, which can range from only 0.01% in frigid winter air in the Arctic to 5% in warm, humid, tropical air. The atmosphere also contains several gases in trace amounts, such as helium, neon, methane and nitrous oxide. One very important trace gas is ozone (O_3), which absorbs harmful UV radiation from the sun.

The earth's atmosphere extends outward to about 1,000 kilometers where it transitions to interplanetary space. However, most of the mass of the atmosphere (greater than 99 percent) is located within the first 40 kilometers. On average, the total weight of the atmospheric mass exerts a pressure at sea level of around 1.0×10^5 pascals (Pa; or one atmosphere), which is equivalent to 1.0 kg per cm^2. The density of the atmospheric mass is much greater close to the surface and decreases rapidly with increasing altitude. The vertical temperature profile of the atmosphere is variable and depends upon the types of radiation that affect each atmospheric layer. This, in turn, depends upon the chemical composition of that layer (mostly involving trace gases). Based on these factors, the atmosphere can be divided into four distinct layers: the troposphere, stratosphere, mesosphere, and thermosphere (Figure 2.4.1). The boundaries of the layers are inexact because they may vary over time and space. Beyond the atmosphere is outer space, an immeasurably vast region where the Earth exerts no detectable chemical or thermal influences.

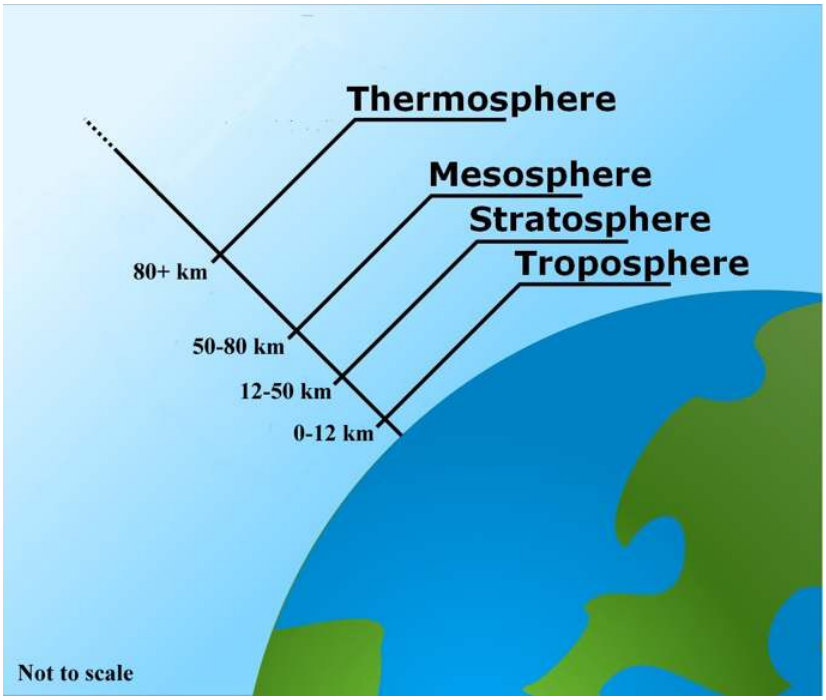


Figure 2.4.1**:** The layers of the atmosphere. the troposphere is the closest to the Earth's surface (0-12 km). Next, is the stratosphere (12-50 km), mesophere (50-80 km), and thermosphere (80+ km). The outermost layer (the exosphere) is not shown. **Ground-level ozone** in the troposphere is a form of air pollution, but the **ozone layer** in the stratosphere helps filter UV rays. "Atmospheric Layers" by GFDL is licensed under CC BY-SA 3.0.

The **troposphere** (or lower atmosphere) contains 85-90% of the atmospheric mass and extends from the surface to an altitude of 8-20 km. It is thinner at high latitudes, and thicker at equatorial latitudes, but also varies seasonally, at any place being thicker during the summer than in the winter. Because convective air currents (winds) are common in the troposphere (the name troposphere means “region of mixing”) it is sometimes referred to as the “weather layer.” It also contains some 99 percent of the total water vapor of the atmosphere. The temperature of the troposphere is warm (roughly 17º C) near the surface of the earth. This is due to the absorption of infrared radiation from the surface by water vapor and other greenhouse gases (e.g. carbon dioxide, nitrous oxide and methane) in the troposphere. The concentration of these gases decreases with altitude, and therefore, the heating effect is greatest near the surface. The temperature in the troposphere decreases at a rate of roughly 6.5º C per kilometer of altitude. The temperature at its upper boundary is very cold (roughly -60º C). Water vapor evaporated from the earth's surface condenses in the cooler upper regions of the troposphere and falls back to the surface as rain. Dust and pollutants injected into the troposphere become well mixed in the layer, but are eventually washed out by rainfall. The troposphere is therefore self cleaning. A narrow zone at the top of the troposphere is called the **tropopause**. It effectively separates the underlying troposphere and the overlying stratosphere. The temperature in the tropopause is relatively constant. Strong eastward winds, known as the **jet stream**, also occur here.

The **stratosphere** extends from the troposphere to as high as about 50 km, depending on the season and latitude. Within the stratosphere there are few convective air currents. The temperature profile of the stratosphere is quite different from that of the troposphere. The temperature remains relatively constant up to roughly 25 kilometers and then gradually increases up to the upper boundary of the layer. The amount of water vapor in the stratosphere is very low, so it is not an important factor in the temperature regulation of the layer. Instead, it is ozone (O3) that causes the observed temperature inversion. Most of the ozone in the atmosphere is contained in a layer of the stratosphere from roughly 20 to 30 kilometers. This ozone layer absorbs solar energy in the form of ultraviolet radiation (UV), and the energy is ultimately dissipated as heat in the stratosphere. This heat leads to the rise in temperature. Stratospheric ozone is also very important for living organisms on the surface of the earth as it protects them by absorbing most of the harmful UV radiation from the sun. The upper boundary of the stratosphere is known as the **stratopause**, which is marked by a sudden decrease in temperature.

The third layer in the earth's atmosphere is called the **mesosphere**. It extends from the stratopause (about 50 kilometers) to roughly 85 kilometers above the earth's surface. Because the mesosphere has negligible amounts of water vapor and ozone for generating heat, the temperature drops across this layer. It is warmed from the bottom by the stratosphere. The air is very thin in this region with a density about 1/1000 that of the surface. With increasing altitude this layer becomes increasingly dominated by lighter gases, and in the outer reaches, the remaining gases become stratified by molecular weight.

The fourth layer, the **thermosphere**, extends outward from about 85 kilometers to about 600 kilometers. Its upper boundary is ill defined. The temperature in the thermosphere increases with altitude, up to 1500º C or more. The high temperatures are the result of absorption of intense solar radiation by the last remaining oxygen molecules. The temperature can vary substantially depending upon the level of solar activity. The lower region of the thermosphere (up to about 550 kilometers) is also known as the **ionosphere**. Because of the high temperatures in this region, gas particles become ionized. The ionosphere is important because it reflects radio waves from the earth's surface, allowing long-distance radio communication. The visual atmospheric phenomenon known as the northern lights also occurs in this region. The outer region of the atmosphere is known as the **exosphere**. The exosphere represents the final transition between the atmosphere and interplanetary space. It extends about 1000 kilometers and contains mainly helium and hydrogen. Most satellites operate in this region.

Climate and Weather both Happen in the Atmosphere

A common misconception about global climate change is that a specific weather event occurring in a particular region (for example, a very cool week in June in central Indiana) is evidence of global climate change. However, a cold week in June is a weather-related event and not a climate-related one. These misconceptions often arise because of confusion over the terms climate and weather. Both long-term climate patterns and short-term weather patterns have to do with conditions in the atmosphere.

Climate refers to the long-term, predictable atmospheric conditions of a specific area. The climate of a biome is characterized by having consistent temperature and annual rainfall ranges. Climate does not address the amount of rain that fell on one particular day in a biome or the colder-than-average temperatures that occurred on one day. Climate scientists often average over decades to determine climate in a given location. **Climate change** refers to any significant change in the measures of climate lasting for an extended period of time. In other words, climate change includes major changes in temperature, precipitation, or wind patterns, among other effects, that occur over several decades or longer. More details about climate can be found in the sections of this book on "Earth's Energy Balance," "What Makes the Climate Change?," and "Past Climate Change."

In contrast, weather refers to the conditions of the atmosphere during a short period of time. Weather forecasts are usually made for 48-hour cycles. Long-range weather forecasts are available but can be unreliable. For more on how Atmospheric and Oceanic Circulation affect weather patterns across the globe, see the section of this book on "Atmospheric and Oceanic Circulation." We won't be covering short-term weather patterns in this text, but there are many good resources for learning more about meteorology including Roland Stull's book Practical Meteorology.

To better understand the difference between climate and weather, imagine that you are planning an outdoor event in northern Wisconsin. You would be thinking about *climate* when you plan the event in the summer rather than the winter because you have long-term knowledge that any given Saturday in the months of May to August would be a better choice for an outdoor event in Wisconsin than any given Saturday in January. However, you cannot determine the specific day that the event should be held on because it is difficult to accurately predict the weather on a specific day. Climate can be considered “average” weather.

Contributors and Attributions

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2.5: Earth's Energy Balance

Earth's Temperature is a Balancing Act

Earth's temperature depends on the balance between energy entering and leaving the planet. When incoming energy from the sun is absorbed, Earth warms. When the sun's energy is reflected back into space, Earth avoids warming. When energy is released from Earth into space, the planet cools. Many factors, both natural and human, can cause changes in Earth's energy balance, including:

- Changes in the greenhouse effect, which affects the amount of heat retained by Earth's atmosphere;
- Variations in the sun's energy reaching Earth;
- Changes in the reflectivity of Earth's atmosphere and surface.

The balance of incoming and outgoing heat on Earth is referred to as its **energy budget**. As with any budget, to maintain constant conditions the budget must be balanced so that the incoming heat equals the outgoing heat. The energy budget of Earth appears below (Figure 2.5.1).

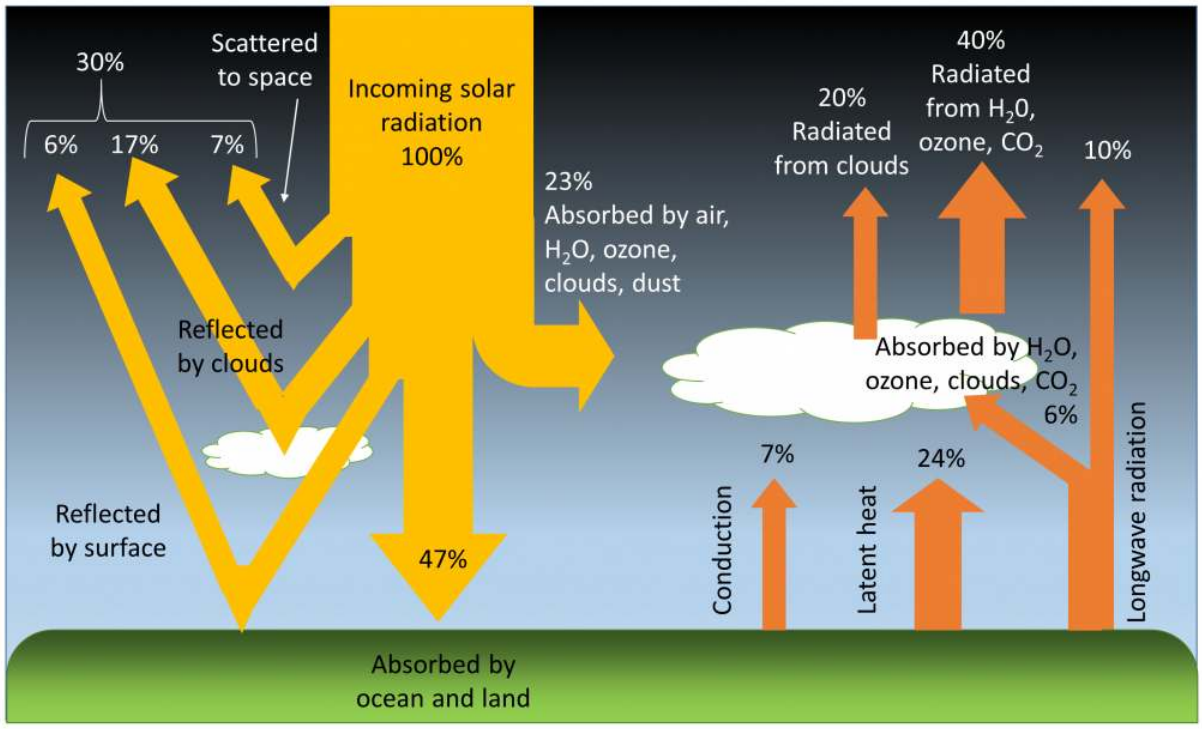


Figure 2.5.1: Earth's energy budget. Of all of the solar radiation reaching Earth, 30% is reflected back to space and 70% is absorbed by the Earth (47%) and atmosphere (23%). The heat absorbed by the land and oceans is exchanged with the atmosphere through conduction, radiation, and latent heat (phase change). The heat absorbed by the atmosphere is eventually radiated back into space. *Source: Paul Webb, Roger Williams University.*

Solar radiation from the sun is composed of mostly ultraviolet (UV), visible light, and infrared (IR) radiation (Figure 2.5.2). Components of solar radiation include parts with a shorter wavelength than visible light, like ultraviolet light, and parts of the spectrum with longer wavelengths, like IR and others (Figure 2.5.2). Of all of the solar energy reaching the Earth, about 30% is reflected back into space from the atmosphere, clouds, and surface of the Earth (Figure 2.5.1). Another 23% of the energy is absorbed by the water vapor, clouds, and dust in the atmosphere, where it is converted into heat.

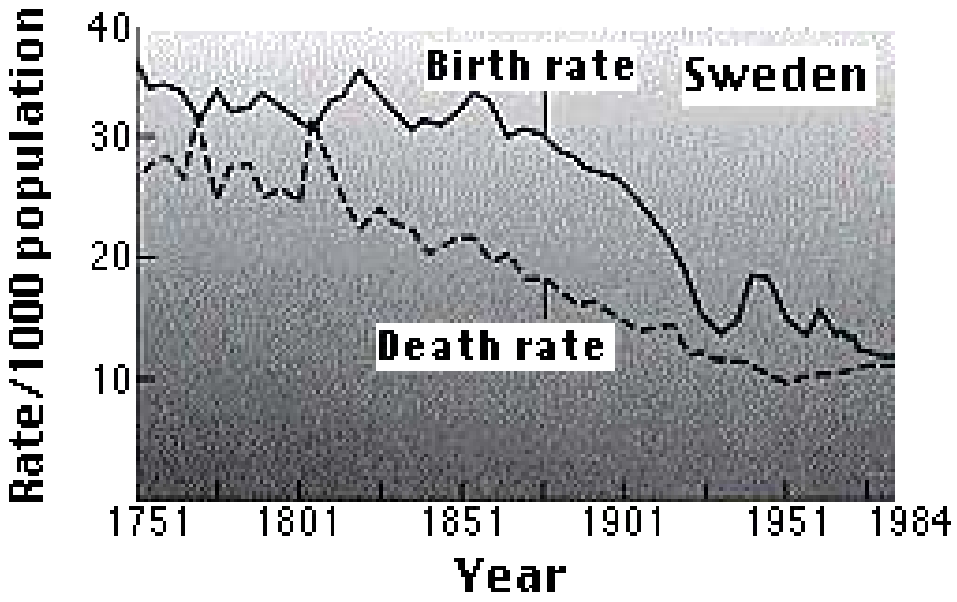


Figure 2.5.2: Incoming radiation absorbed, scattered, and reflected by atmospheric gases.

Just under half (47%) of the incoming solar radiation is absorbed by the land and ocean, and this energy heats up the Earth's surface. The energy absorbed by the Earth returns to the atmosphere through three processes; conduction, radiation, and latent heat (phase change) (Figure 2.5.1).

Conduction is the transfer of heat through direct contact between the surface and the atmosphere. Air is a relatively poor thermal conductor (which means it is a good insulator), so conduction represents only a small part of the energy transfer between the Earth and the atmosphere; equal to about 7% of the incoming solar energy.

All bodies with a temperature above absolute zero (-273° C) radiate heat in the form of longwave, infrared **radiation** (Figure 2.5.2). The warmed Earth is no exception, and about 16% of the original solar energy is radiated from the Earth to the atmosphere (Figure 2.5.1). When sunlight warms a surface such as a paved surface, a patio, or deck, the warmer surface emits more thermal radiation, which is a type of IR radiation. So, there is a conversion from visible, UV, and IR to just thermal IR. This thermal IR is what we experience as heat. Some of this radiated energy will dissipate into space, but a significant amount of heat will be absorbed by the atmosphere. This is the basis for the **greenhouse effect** (Figure 2.5.3). In the greenhouse effect, shortwave solar radiation passes through the atmosphere and reaches the Earth's surface where it gets absorbed. When the radiation is re-emitted by the Earth, it is now in the form of long wavelength, infrared radiation, which does not easily pass through the atmosphere. Instead, this infrared radiation is absorbed by the atmosphere, particularly by the greenhouse gases such as CO_2, methane, and water vapor. As a result, the atmosphere heats up. Some of the infrared radiation absorbed by the atmosphere is also re-emitted back to the planet's surface, further increasing warming. Without the greenhouse effect, the average temperature on Earth would be about -18° C, which is too cold for liquid water, and therefore life as we know it could not exist!

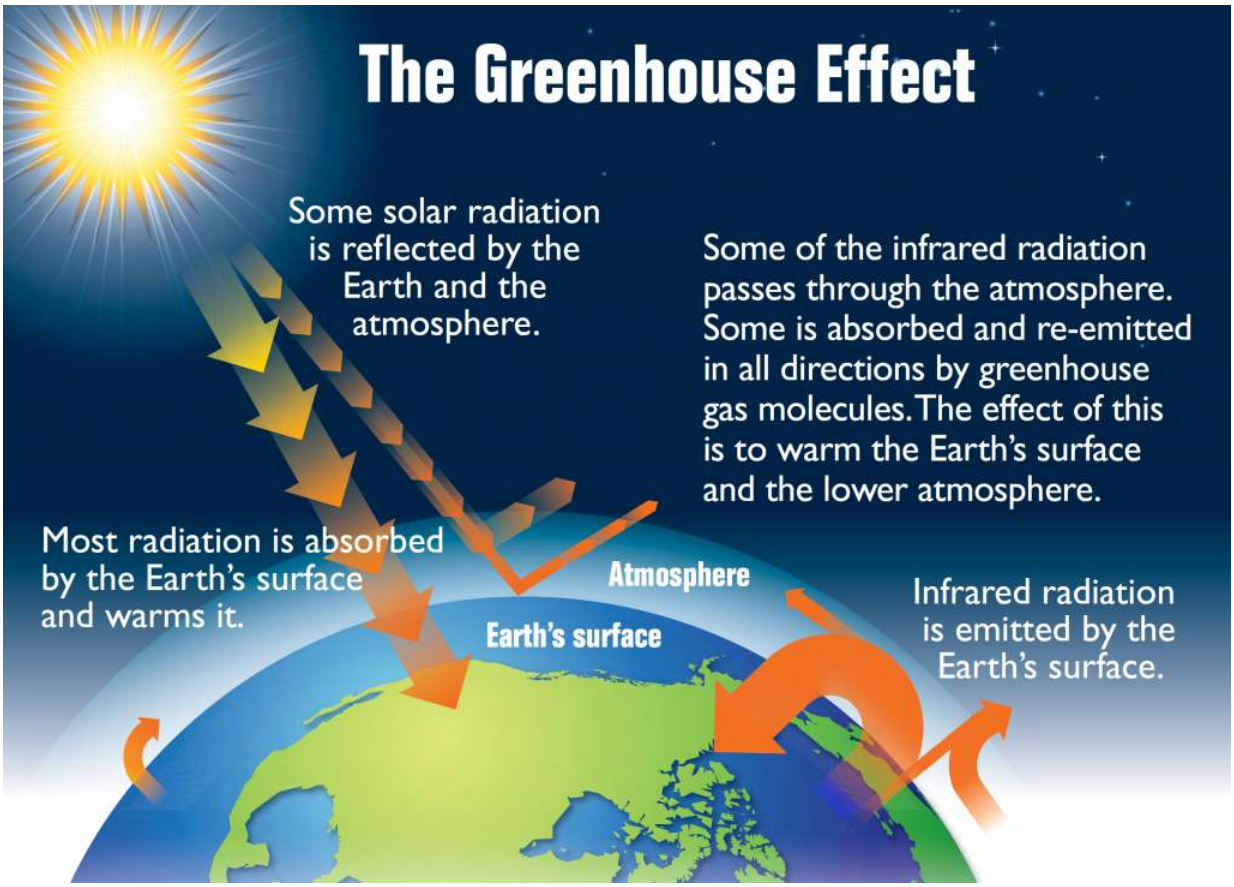


Figure 2.5.3**:** An explanation of the greenhouse effect. "Earth's Greenhouse Effect" by US EPA is available in the public domain.

The largest pathway for energy exchange between the land or oceans and the atmosphere is **latent heat** transferred through **phase changes**; heat released or absorbed when water moves between solid, liquid, and vapor forms. Heat must be added to liquid water to make it evaporate, and when water vapor is formed, that heat is removed from the ocean and transferred to the atmosphere along with the water vapor. When water vapor condenses into rain, that heat is then returned to the oceans. The same process happens with the formation and melting of ice. Heat is absorbed by ice when it melts, and heat is released when ice forms, and these phase changes transfer heat between the oceans and the atmosphere.

To complete the energy budget, the heat that is absorbed by the atmosphere either directly from solar radiation or as a result of conduction, radiation and latent heat, is eventually radiated back into space (Figure 2.5.1).

Greenhouse Gasses

Throughout this chapter we will be talking about the role of **greenhouse gases** (GHGs) in controlling the climate, so it is important to understand what greenhouse gases are and how they work. As you know, the dominant gases of the atmosphere are nitrogen (as N_2) and oxygen (as O_2). These gas molecules have only two atoms each and are not GHGs. Some of the other important gases of the atmosphere are water vapor (H_2O), carbon dioxide (CO_2), and methane (CH_4). All of these have more than two atoms, and they are GHGs. (For more information on the relative amounts of different gasses in the atmosphere, see Atmosphere). All molecules vibrate at various frequencies and in various ways, and some of those vibrations take place at frequencies within the range of the infrared (IR) radiation that is emitted by Earth's surface. Gases with two atoms, such as O_2, can only vibrate by stretching (back and forth), and those vibrations are much faster than the IR radiation (Figure 2.5.4). Gases with three or more atoms (such as CO_2) vibrate by stretching as well, but they can also vibrate in other ways, such as by bending (Figure 2.5.4). Those vibrations are slower and match IR radiation frequencies. When IR radiation interacts with CO_2 or with one of the other GHGs, the molecular vibrations are enhanced because there is a match between the wavelength of the IR light and the vibrational frequency of the molecule. This makes the molecule vibrate more vigorously, heating the surrounding air in the process. These molecules also emit IR radiation in

all directions, some of which reaches Earth's surface. The heating caused by the more vigorous vibrations of GHGs is the **greenhouse effect**.

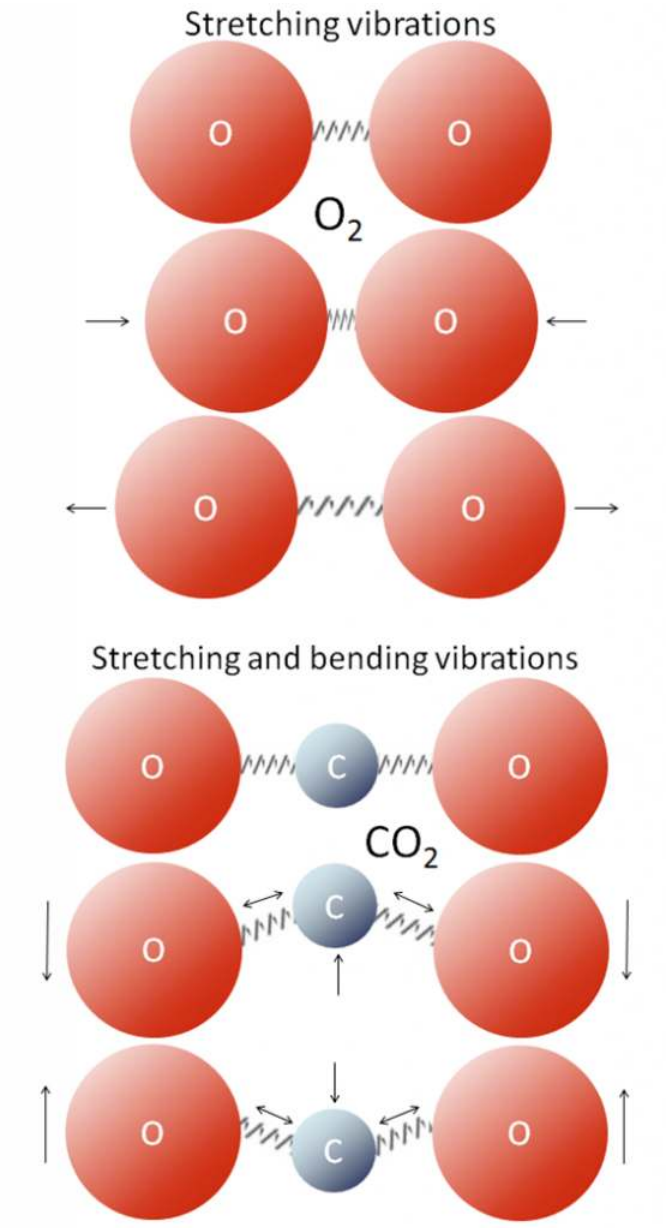


Figure 2.5.4: Stretching versus bending vibrations in atmospheric gases. Image by Steven Earle is licensed under CC BY.

Differential Heating of Earth's Surface

If the Earth was a flat surface facing the sun, every part of that surface would receive the same amount of incoming solar radiation. However, because the Earth is a sphere, sunlight is not equally distributed over the Earth's surface, so different regions of Earth will be heated to different degrees. This differential heating of Earth's surface occurs for a number of reasons. First, because of the curvature of Earth, sunlight only falls perpendicularly to the surface at the center of the sphere (equatorial regions). At any other point on Earth, the angle between the surface and the incoming solar radiation is less than 90°. Because of this, the same amount of incoming solar radiation will be concentrated in a smaller area at the equator, but will be spread over a much larger area at the poles (Figure 2.5.5). Thus the tropics receive more intense sunlight and a greater amount of heating per unit of area than the polar regions. The angle at which sunlight strikes the Earth contributes to differential heating of the surface in an additional way. At the poles, because of the angle at which the solar energy strikes the surface, more of the light will glance off of the surface and the

atmosphere and be reflected back into space. At the equator, the direct angle with which light reaches the surface results in more of the energy being absorbed by the earth rather than being reflected (bouncing off the surface). Recall that the earth is also tilted, changing which part of the earth's surface is pointed directly at the sun during different seasons (see What Makes the Climate Change for more on Earth's Tilt).

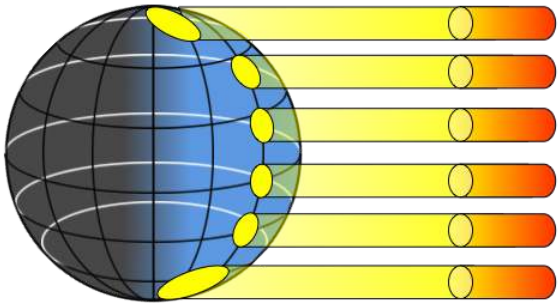


Figure 2.5.5**:** Because of the curvature of the Earth, the same amount of sunlight will be spread out over a larger area at the poles compared to the equator. The equator therefore receives more intense sunlight, and a greater amount of heat per unit of area. "Solar Angle of Incidence on Earth" by Thebiologyprimer is available in the public domain.

Finally, the poles reflect more solar energy than other parts of the Earth because the poles have a higher **albedo**. The albedo refers to reflectivity of a surface, expressed as the percentage of light that reflects off a given material. Lighter surfaces are more reflective than darker surfaces (which absorb more energy), and therefore have a higher albedo. Water in the oceans or on a lake is one of the darkest surfaces, reflecting less than 10% of the incident light, while clouds and snow or ice are among the brightest surfaces, reflecting 70% to 90% of the incident light (Figure 2.5.6).

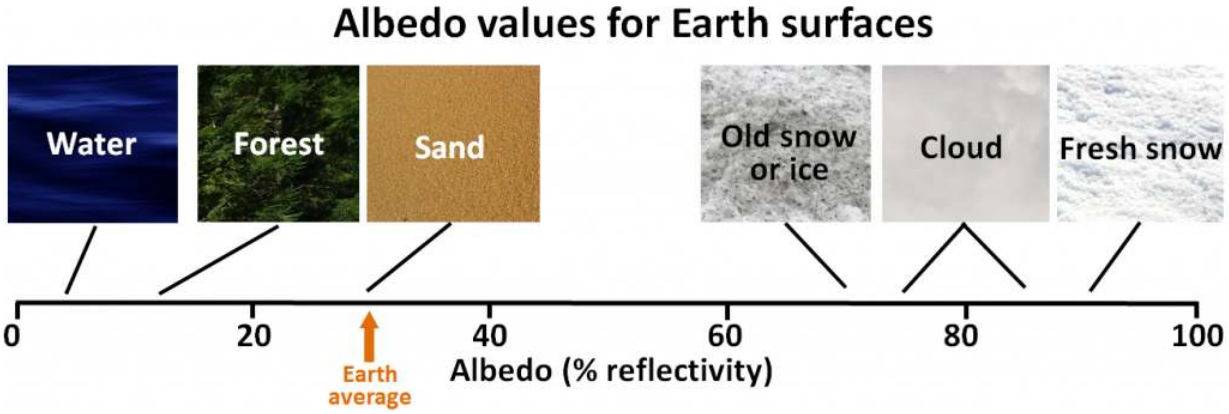


Figure 2.5.6: Typical albedo values for Earth surfaces. Image by Steven Earle is licensed under CC BY.

At the poles, the ice, snow and cloud cover create a much higher albedo, and the poles reflect more and absorb less solar energy than the lower latitudes (Figure 2.5.7). Through all of these mechanisms, the poles absorb much less solar radiation than equatorial regions, which is why the poles are cold and the tropics are very warm.

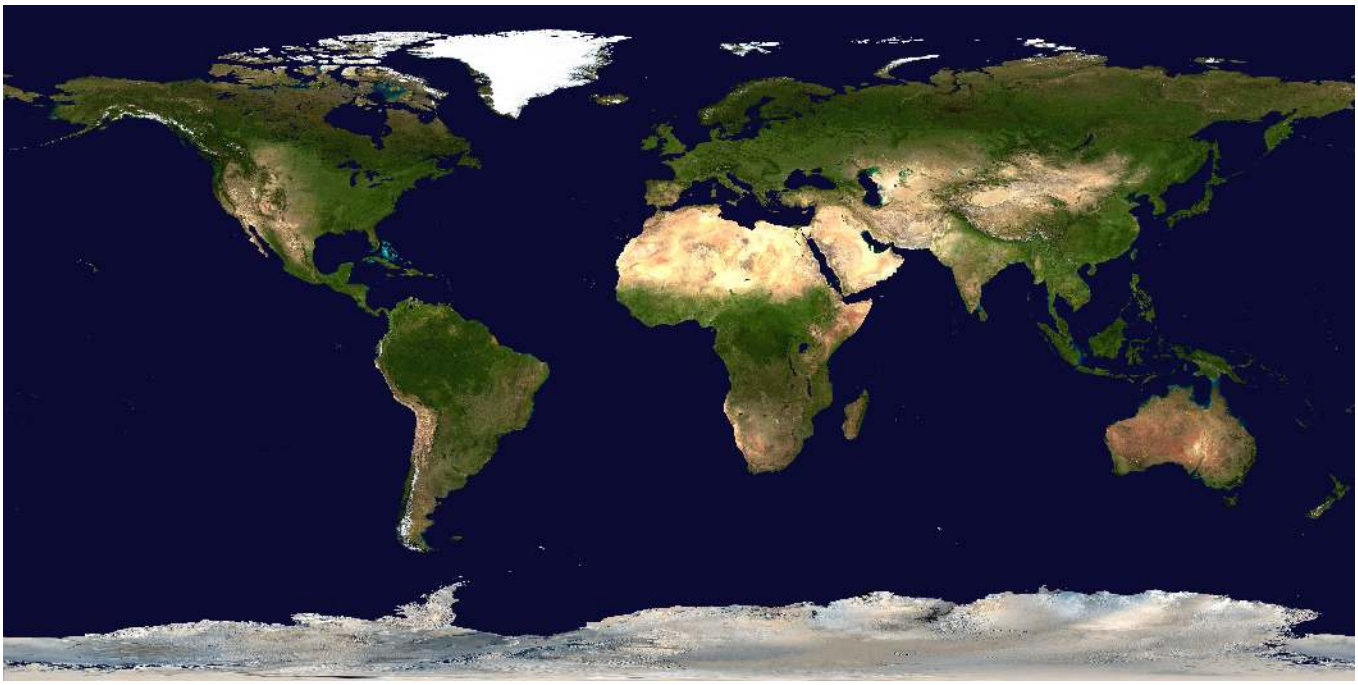


Figure 2.5.7: **Surface of Earth with Cloud Cover Removed** -- The surface of the Earth with cloud cover removed. The poles and deserts are much brighter than the oceans and forests. *Source: NASA Goddard Space Flight Center Image by Reto Stöckli. Courtesy of NASA's Earth Observatory.*

But there is an interesting twist to this global distribution of heat. The tropical regions actually receive more radiant heat than they emit, and the poles emit more heat than they receive (Figure 2.5.8). We should therefore expect that the tropics will be getting continually warmer, while the poles become increasingly cold. Yet this is not the case; so what is happening? Rather than the heat remaining isolated near the equator, about 20% of the heat from the tropics is transported to the poles before it is emitted. This large scale transport of energy moderates the climates at both extremes. The mechanisms for this heat transfer are ocean and atmospheric circulation.

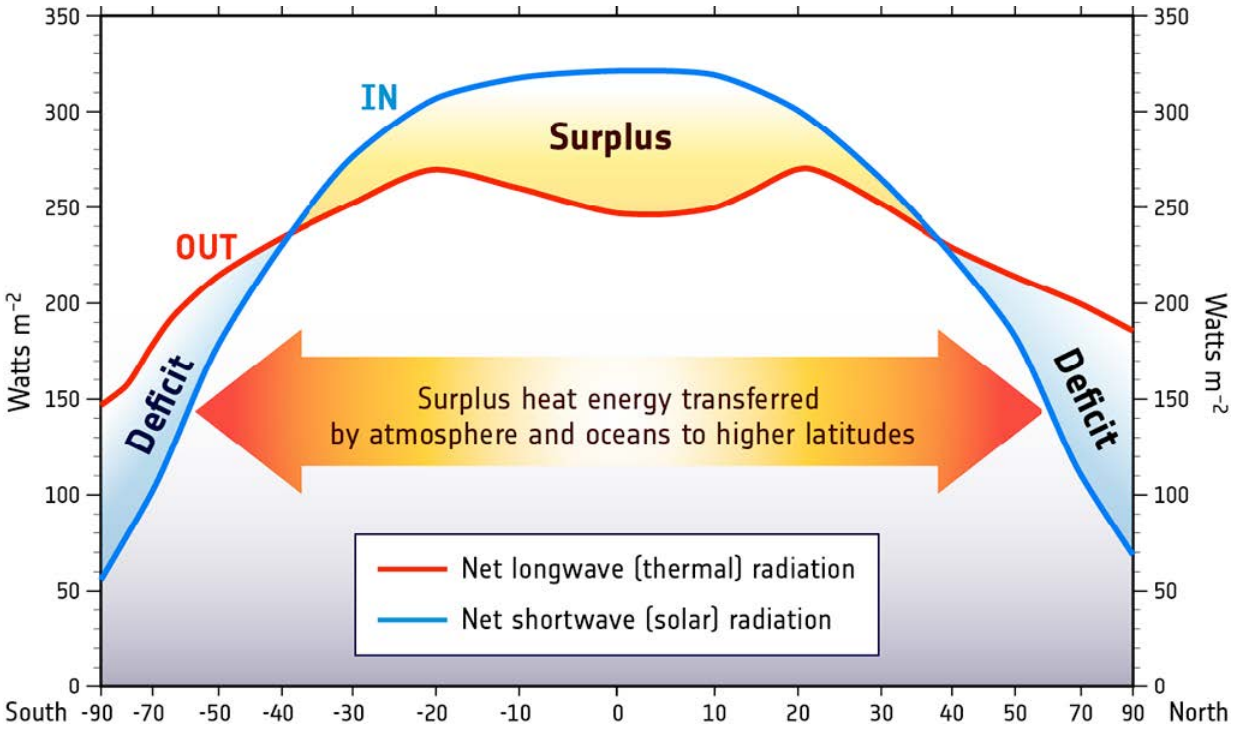


Figure 2.5.8: The balance between heat gain and heat loss as a function of latitude. Excess heat received near the equator is transferred towards the poles *Source: National Oceanography Centre (NOC).*

The Earth's Tilt causes Seasons

One of the fundamental facts of life at Earth's mid-latitudes, is that there are significant variations in the heat we receive from the Sun during the course of the year. The difference between seasons gets more pronounced the farther north or south from the equator we travel, and the seasons in the Southern Hemisphere are the opposite of what we find on the northern half of Earth. The seasons are actually caused by the 23.5° tilt of Earth's axis which continues to point the same direction in the sky throughout the year (figure 2.5.9). As Earth travels around the Sun, in June the Northern Hemisphere "leans into" the Sun and is more directly illuminated. In December, the situation is reversed: the Southern Hemisphere leans into the Sun, and the Northern Hemisphere leans away. In September and March, Earth leans "sideways"—neither into the Sun nor away from it—so the two hemispheres are equally favored with sunshine. When we lean into the Sun, sunlight hits us at a more direct angle and is more effective at heating Earth's surface (figure 2.5.10). During the summer season, the sun also spends more time above the horizon, resulting in more energy hitting the surface of the Earth.

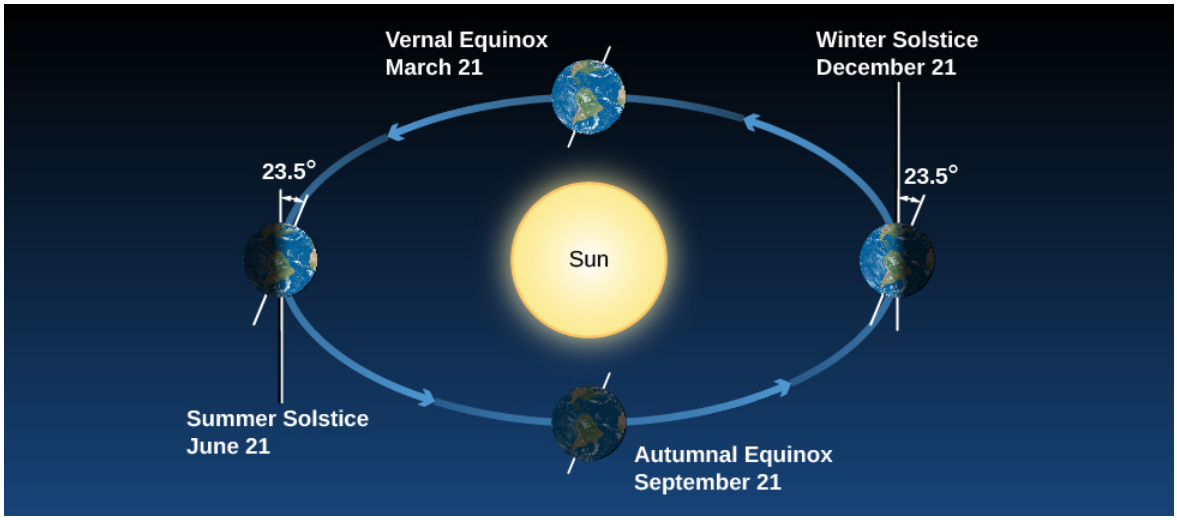


Figure 2.5.9: We see Earth at different seasons as it circles the Sun. In June, the Northern Hemisphere "leans into" the Sun, and those in the North experience summer and have longer days. In December, during winter in the Northern Hemisphere, the Southern Hemisphere "leans into" the Sun and is illuminated more directly. In spring and autumn, the two hemispheres receive more equal shares of sunlight. *Source: 4.2: The Seasons.*

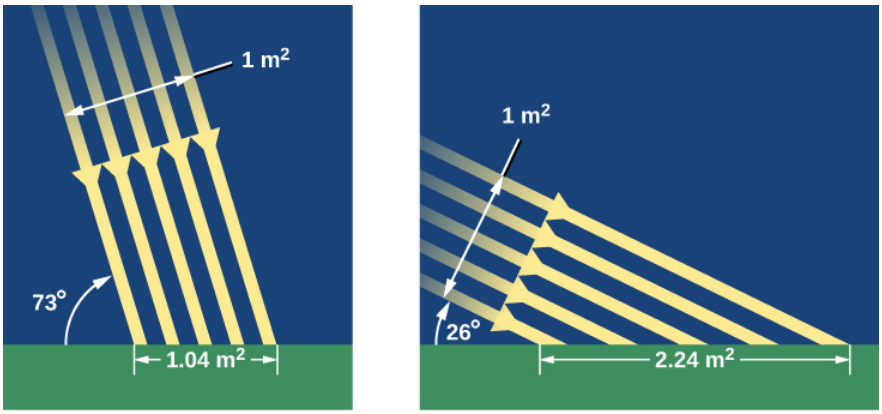


Figure 2.5.10: The Sun's Rays in Summer and Winter. (a) In summer, the Sun appears high in the sky and its rays hit Earth more directly, spreading out less. (b) In winter, the Sun is low in the sky and its rays spread out over a much wider area, becoming less effective at heating the ground. *Source: 4.2: The Seasons.*

Further Reading

The National Aeronautical and Space Administration (NASA) Earth Observatory website has an array of climate resources. For a more in-depth discussion of Earth's energy budget, go to http://earthobservatory.nasa.gov/Features/EnergyBalance/

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2.6: Atmospheric and Oceanic Circulation

Atmospheric Circulation

Differential heating of the Earth's surface results in equatorial regions receiving more heat than the poles. As air is warmed at the equator it becomes less dense and rises, while at the poles the cold air is denser and sinks. If the Earth was non-rotating, the warm air rising at the equator would reach the upper atmosphere and begin moving horizontally towards the poles. As the air reached the poles it would cool and sink, and would move over the surface of Earth back towards the equator. This would result in one large atmospheric convection cell in each hemisphere (Figure 2.6.1), with air rising at the equator and sinking at the poles, and the movement of air over the Earth's surface creating the winds. On this non-rotating Earth, the prevailing winds would thus blow from the poles towards the equator in both hemispheres (Figure 2.6.1).

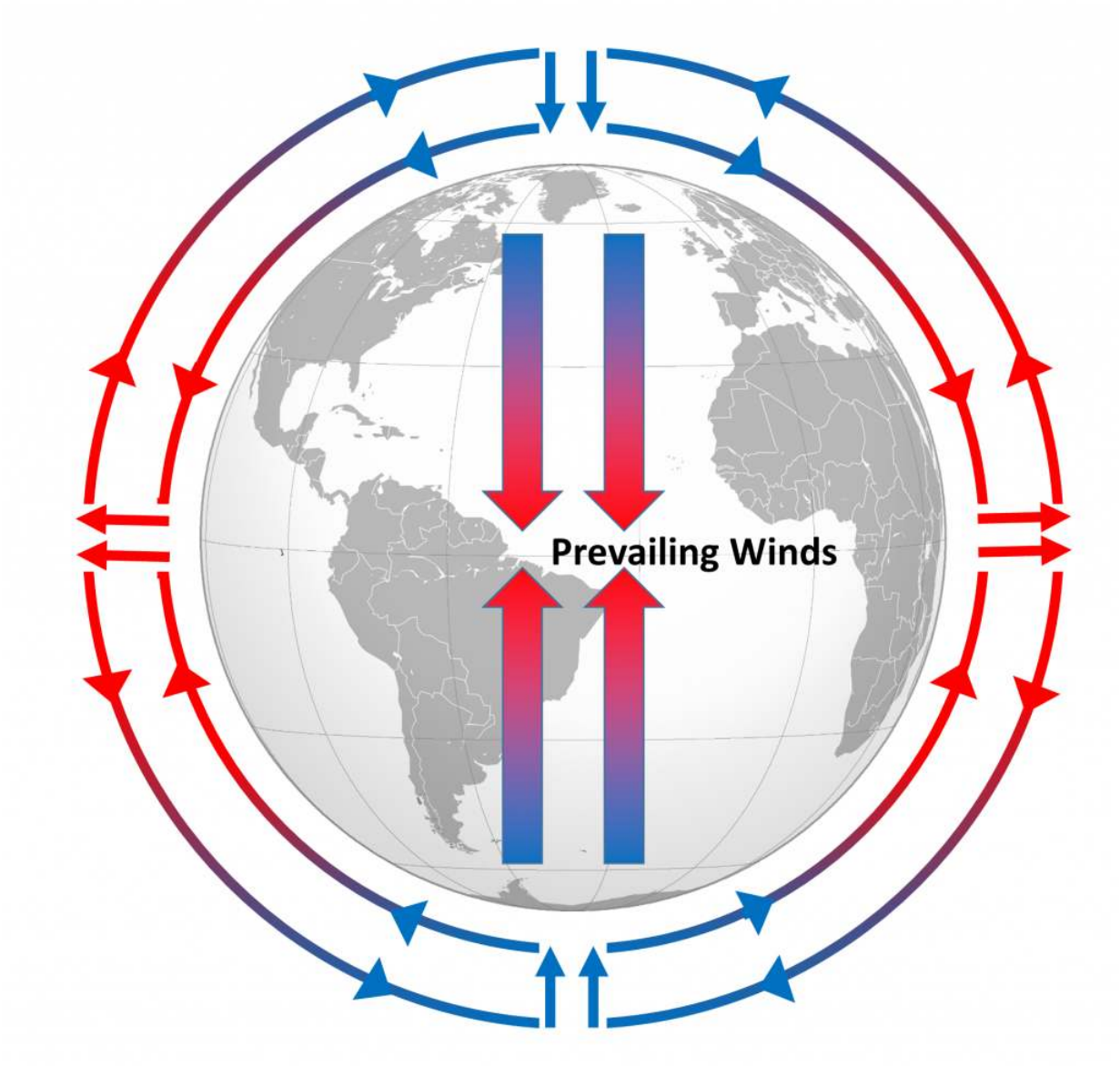


Figure 2.6.1: Hypothetical atmospheric convection cells on a non-rotating Earth. Air rises at the equator and sinks at the poles, creating a single convection cell in each hemisphere. The prevailing winds moving over the Earth's surface blow from the poles towards the equator in both hemispheres (Modified by Paul Webb from globe image by Location_of_Cape_Verde_in_the_globe.svg: Eddo derivative work: Luan fala! [CC BY-SA 3.0], via Wikimedia Commons).

The non-rotating situation in Figure (2.6.1) is of course only hypothetical, and in reality the Earth's rotation makes this atmospheric circulation a bit more complex. The paths of the winds on a rotating Earth are deflected by the **Coriolis Effect**. The Coriolis Effect is a result of the fact that different latitudes on Earth rotate at different speeds. This is because every point on Earth must make a complete rotation in 24 hours, but some points must travel farther, and therefore faster, to complete the rotation in the same amount of time. In 24 hours a point on the equator must complete a rotation distance equal to the circumference of the Earth, which is about 40,000 km. A point right on the poles covers no distance in that time; it just spins. So the speed of rotation at the equator is about 1600 km/hr, while at the poles the speed is 0 km/hr. Latitudes in between rotate at intermediate speeds; approximately 1400 km/hr at 30° and 800 km/hr at 60°. As objects move over the surface of the Earth they encounter regions of varying speed, which causes their path to be deflected by the Coriolis Effect.

To explain the Coriolis Effect, imagine a cannon positioned at the equator and facing north. Even though the cannon appears stationary to someone on Earth, it is in fact moving east at about 1600 km/hr due to Earth's rotation. When the cannon fires the projectile travels north towards its target; but it also continues to move to the east at 1600 km/hr, the speed it had while it was still in the cannon. As the shell moves over higher latitudes, its momentum carries it eastward faster than the speed at which the ground beneath it is rotating. For example, by 30° latitude the shell is moving east at 1600 km/hr while the ground is moving east at only 1400 km/hr. Therefore, the shell gets "ahead" of its target, and will land to the east of its intended destination. From the point of view of the cannon, the path of the projectile appears to have been deflected to the right (red arrow, Figure 2.6.2). Similarly, a cannon located at 60° and facing the equator will be moving east at 800 km/hr. When its shell is fired towards the equator, the shell will be moving east at 800 km/hr, but as it approaches the equator it will be moving over land that is traveling east *faster* than the projectile. So the projectile gets "behind" its target, and will land to the west of its destination. But from the point of view of the cannon facing the equator, the path of the shell still appears to have been deflected to the right (green arrow, Figure 2.6.2). Therefore, in the Northern Hemisphere, the apparent Coriolis deflection will *always* be to the **right**.

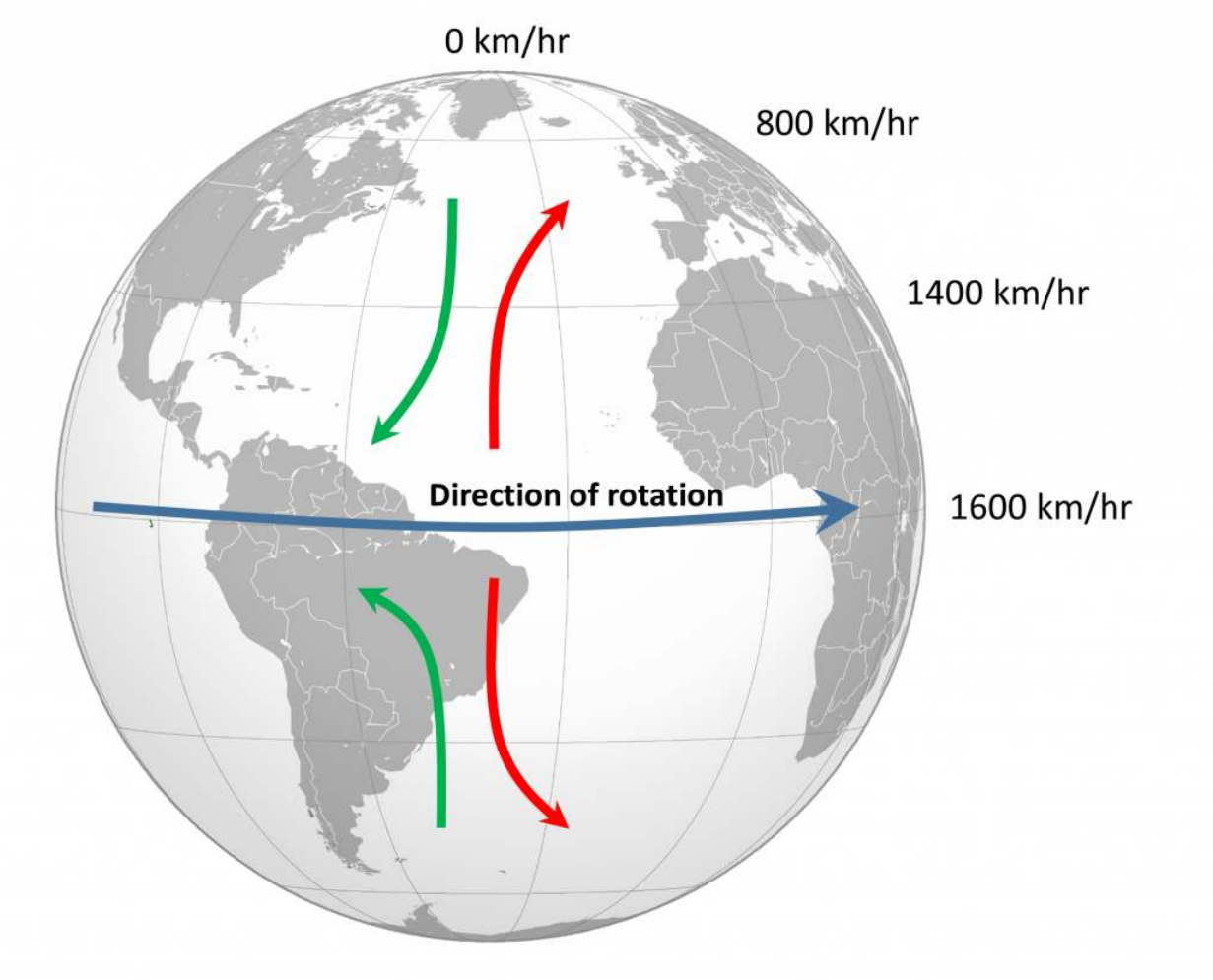


Figure 2.6.2: The Coriolis Effect. Objects moving from the equator towards the poles (red arrows) move into a region of slower rotational speed and their paths are deflected "ahead" of their point of origin. Movement from high latitudes to low latitudes (green arrows) goes from a region of low speed to a region of higher rotation speed, and there is deflection "behind" their point of origin. In the Northern Hemisphere this deflection is always to the right from the point of origin, and in the Southern Hemisphere the deflection is always to the left
(Modified by Paul Webb from globe image by Location_of_Cape_Verde_in_the_globe.svg: Eddo derivative work: Luan fala! [CC BY-SA 3.0], via Wikimedia Commons).

In the Southern Hemisphere the situation is reversed (Figure 2.6.2). Objects moving towards the equator from the south pole are moving from low speed to high speed, so are left behind and their path is deflected to the left. Movement from the equator towards the south pole also leads to deflection to the left. In the Southern Hemisphere, the Coriolis deflection is always to the **left** from the point of origin.

The magnitude of the Coriolis deflection is related to the difference in rotation speed between the start and end points. Between the poles and 60º latitude, the difference in rotation speed is 800 km/hr. Between the equator and 30º latitude, the difference is only 200 km/hr (Figure 2.6.2). Therefore the strength of the Coriolis Effect is stronger near the poles, and weaker at the equator.

Because of the rotation of the Earth and the Coriolis Effect, rather than a single atmospheric convection cell in each hemisphere, there are three major cells per hemisphere. Warm air rising at the equator cools as it moves through the upper atmosphere, and it descends at around 30º latitude. The convection cells created by rising air at the equator and sinking air at 30º are referred to as **Hadley Cells**, of which there is one in each hemisphere. The cold air that descends at the poles moves over the Earth's surface towards the equator, and by about 60º latitude it begins to rise, creating a **Polar Cell** between 60º and 90º. Between 30º and 60º lie the **Ferrel Cells**, composed of sinking air at 30º and rising air at 60º (Figure 2.6.3). With three convection cells in each hemisphere that rotate in alternate directions, the surface winds no longer always blow from the poles towards the equator as in the non-rotating

Earth in Figure 2.6.1. Instead, surface winds in both hemispheres blow towards the equator between 90° and 60° latitude, and between 0° and 30° latitude. Between 30° and 60° latitude, the surface winds blow towards the poles (Figure 2.6.3).

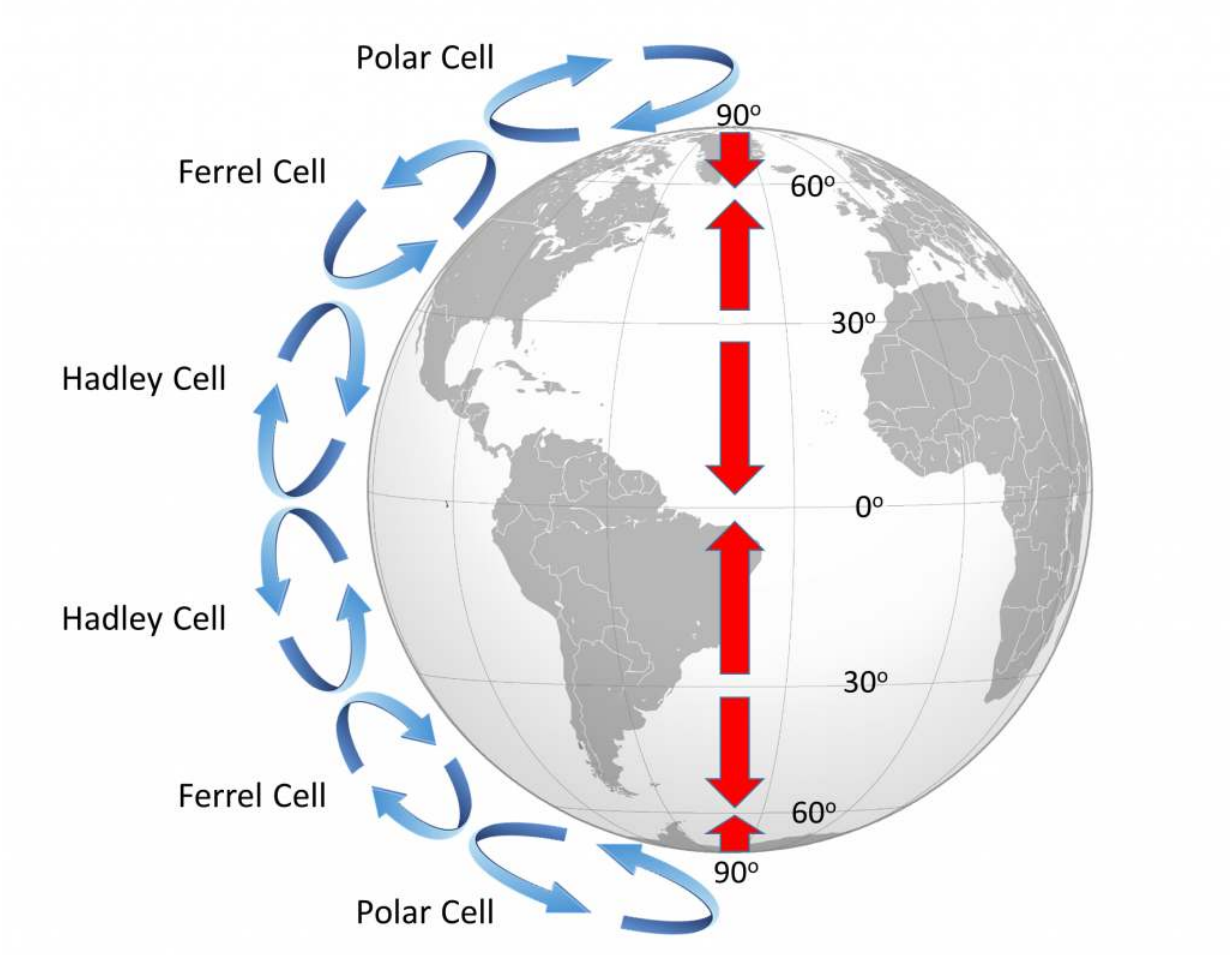


Figure 2.6.3: On a rotating Earth, there are three atmospheric convection cells in each hemisphere, leading to alternating bands of surface winds (red arrows)
(Modified by Paul Webb from globe image by Location_of_Cape_Verde_in_the_globe.svg: Eddo derivative work: Luan fala! [CC BY-SA 3.0], via Wikimedia Commons).

The surface winds created by the atmospheric convection cells are also influenced by the Coriolis Effect as they change latitudes. The Coriolis Effect deflects the path of the winds to the right in the Northern Hemisphere and to the left in the Southern Hemisphere. Adding this deflection leads to the pattern of prevailing winds illustrated in Figure 2.6.4). Between the equator and 30° latitude are the **trade winds**; the northeast trade winds in the Northern Hemisphere and the southeast trade winds in the Southern Hemisphere (note that winds are named based on the direction from which they originate, not where they are going). The **westerlies** are the dominant winds between 30° and 60° in both hemispheres, and the **polar easterlies** are found between 60° and the poles.

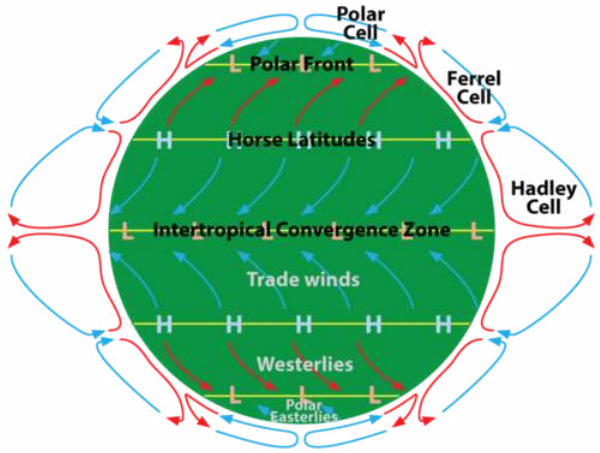


Figure 2.6.4: The atmospheric circulation cells, showing direction of winds at Earth's surface. The atmosphere is thicker at the equator than at the poles. *Created by Zachary Wilson for CK-12 Foundation CC BY-NC 3.0.*

In between these wind bands lie regions of high and low pressure. High pressure zones occur where air is descending, while low pressure zones indicate rising air. Along the equator the rising air creates a low pressure region called the **doldrums**, or the **Intertropical Convergence Zone** (**ITCZ**) (convergence zone because this is where the trade winds converge). The **doldrums** refer to regions of low pressure around the equator. In these areas, air is rising rather than moving horizontally, so these regions commonly encounter very light winds. The lack of wind could leave sailing ships becalmed for days or weeks at a time, which was not good for the morale of the ship's crew. At 30° latitude there are high pressure zones of descending air known as the **horse latitudes**, or the subtropical highs. Like the doldrums the **horse latitudes** are also areas with light winds, this time due to descending air, which could leave ships becalmed. The term **trade winds** may have originally derived from the terms for "track" or "path", but the term may have become more common during European exploration and commercialization of the New World. Mariners sailing from Europe to the New World could sail south until they reached the trade winds, which would then propel their ships across the Atlantic to the Caribbean. To return to Europe, ships could sail to the northeast until they entered the westerlies, which would then steer them back to Europe. Finally, at 60° lies another low pressure region called the **polar front**. It should be noted that these high and low pressure zones are not fixed in place; their latitude fluctuates depending on the season, and these fluctuations have important implications for regional climates.

In addition to their role in creating the surface winds, these high and low pressure systems also influence other climatic phenomena (Figure 2.6.5). Along the equator air is rising as it is warmed by solar radiation. Warm air contains more water vapor than cold air, which is why we experience humidity during the summer and not during the winter. The water content of air roughly doubles with every 10° C increase in temperature. So the air rising at the equator is warm and full of water vapor; as it rises into the upper atmosphere it cools, and the cool air can no longer hold as much water vapor, so the water condenses and forms rain. Therefore, low pressure systems are associated with precipitation, and we see wet habitats like tropical rainforests near the equator (Figure 2.6.5). The ITCZ migrates slightly with the season, following the relative motion of sunlight between the Tropic of Cancer and Tropic of Capricorn. Because land areas heat more quickly than the oceans and there are more land areas in the Northern Hemisphere, during the Northern Hemisphere's summer, the ITCZ is approximately 5 degrees north of the equator, while in the winter, it shifts back and is approximately at the equator. As the ITCZ shifts, the dominant wind belts also shift slightly north in summer and south in winter, which causes the wet and dry seasons in this area.

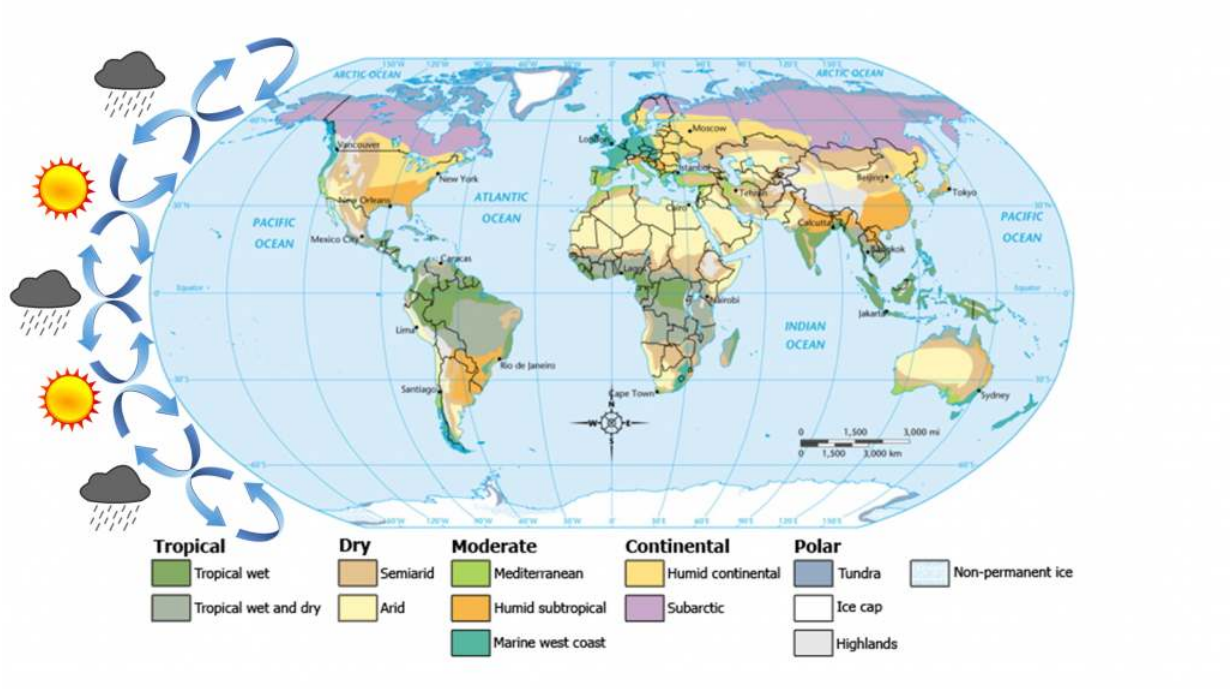


Figure 2.6.5: Major global climatic regions in relation to atmospheric convection cells. Rising air and low pressure creates rain and wet environments at 0° and 60° latitudes, while high pressure, sinking air creates drier conditions at 30° and 90° latitudes. (Modified by Paul Webb; Map by Waitak at en.Wikipedia Later version(s) were uploaded by Splette at en.Wikipedia; Sun by Inductiveload (Own work Based on File:Nuvola_apps_kweather.svg); Raincloud by Calusarul (Own work); all [CC BY-SA 3.0], via Wikimedia Commons).

After rising and producing rain near the equator, the air masses move towards 30° latitude and sink back towards Earth as part of the Hadley convection cells. This air has lost most of its moisture after producing the equatorial rains, so the sinking air is dry, resulting in arid climates near 30° latitude in both hemispheres. Many of the major desert regions on Earth are located near 30° latitude, including much of Australia, the Middle East, and the Sahara Desert of Africa (Figure 2.6.5). The air also becomes compressed and heats up as it sinks, absorbing any moisture from the clouds and creating clear skies. Thus high pressure systems are associated with dry weather and clear skies. This cycle of high and low pressure regions continues with the Ferrel and Polar convection cells, leading to rain and the boreal forests at 60° latitude in the Northern Hemisphere (there are no corresponding large land masses at these latitudes in the Southern Hemisphere). At the poles, descending, dry air produces little precipitation, leading to the polar desert climate.

The elevation of the land also plays a role in precipitation and climactic characteristics. As moist air moves over land and encounters mountains it rises, expands, and cools because of the declining pressure and temperature. The cool air holds less water vapor, so condensation occurs and rain falls on the windward side of the mountains (Figure 2.6.6). As the air passes over the mountains to the leeward side, it is now dry air, and as it sinks the pressure increases, it heats back up, any moisture revaporizes, and it creates dry, deserts regions behind the mountains (Figure 2.6.6). This phenomenon is referred to as a **rain shadow**, and can be found in areas such as the Tibetan Plateau and Gobi Desert behind the Himalayas, Death Valley behind the Sierra Nevada mountains, and the dry San Joaquin Valley in California.

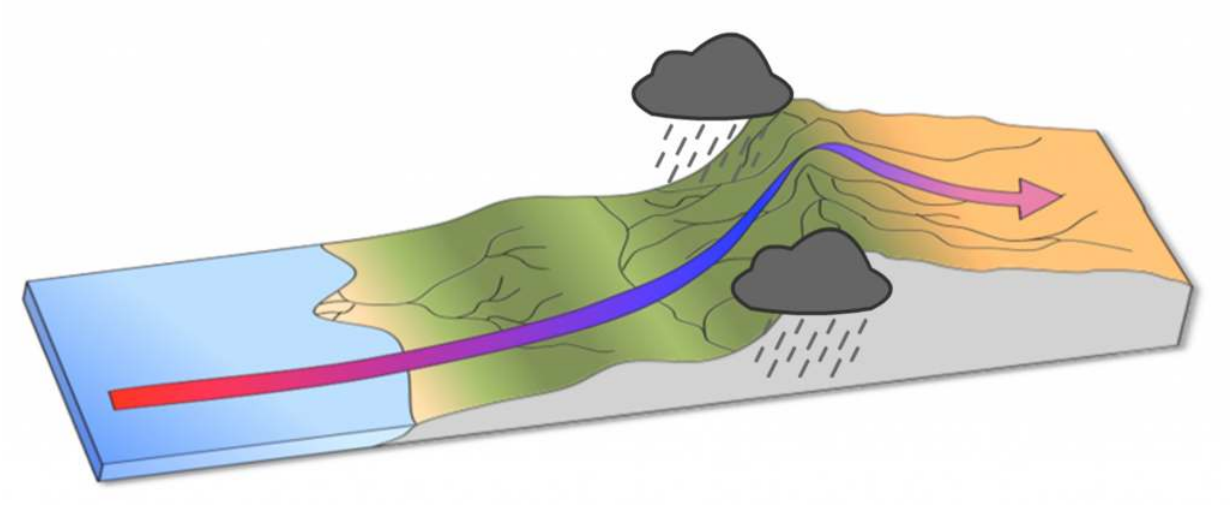


Figure 2.6.6: A rain shadow. Air rising over mountains cools and condenses and forms rain, leaving dry descending air and arid conditions on the other side of the mountain. *Modified by Paul Webb from Thebiologyprimer, public domain via Wikimedia Commons.*

Ocean Circulation

Not unexpectedly, the oceans are warmest near the equator—typically 25° to 30°C—and coldest near the poles—around 0°C (Figure 2.6.7). (Sea water will remain unfrozen down to about -2°C) Variations in sea-surface temperatures (SST) are related to redistribution of water by ocean currents, as we will see below. A good example of that is the plume of warm Gulf Stream water that extends across the northern Atlantic. St. John's, Newfoundland, and Brittany in France are at about the same latitude (47.5° N), but the average SST in St. John's is a frigid 3°C, while that in Brittany is a reasonably comfortable 15°C.

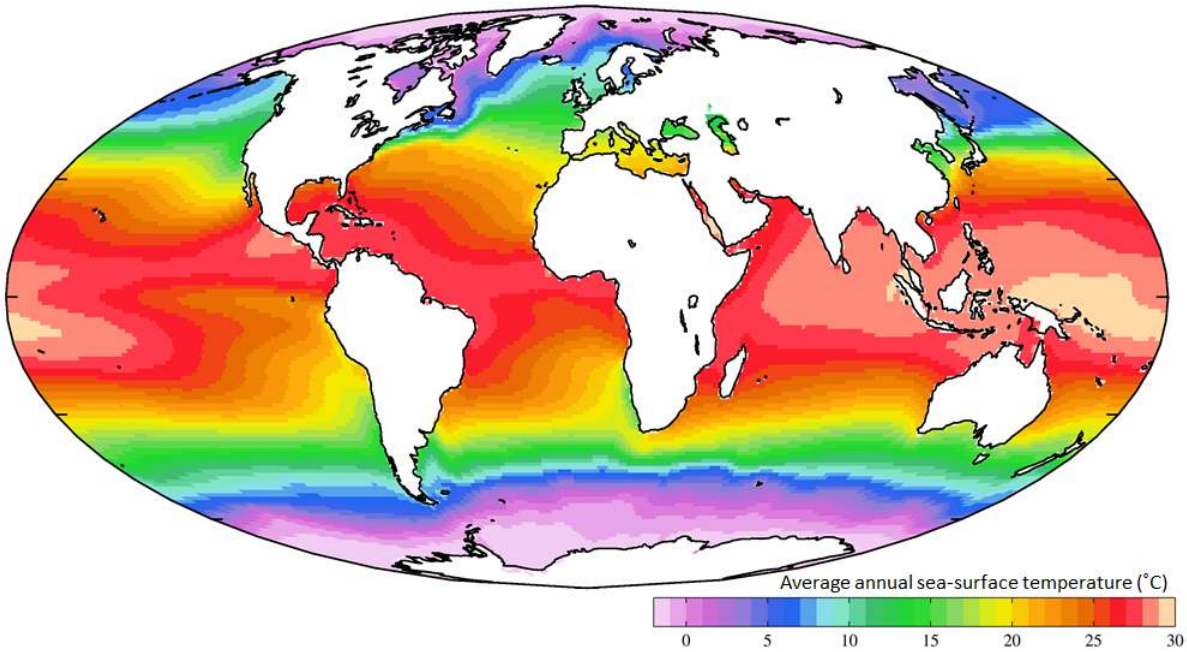


Figure 2.6.7: The global distribution of average annual sea-surface temperatures.
Source: Plumbago, licensed under CC BY-SA.

Currents in the open ocean are created by wind moving across the water and by density differences related to temperature and salinity. An overview of the main ocean currents is shown in Figure 2.6.8. As you can see, the northern hemisphere currents form circular patterns (**gyres**) that rotate clockwise, while the southern hemisphere gyres are counter-clockwise. This happens for the

same reason that the water in your northern hemisphere sink rotates in a clockwise direction as it flows down the drain; this is caused by the **Coriolis effect**.

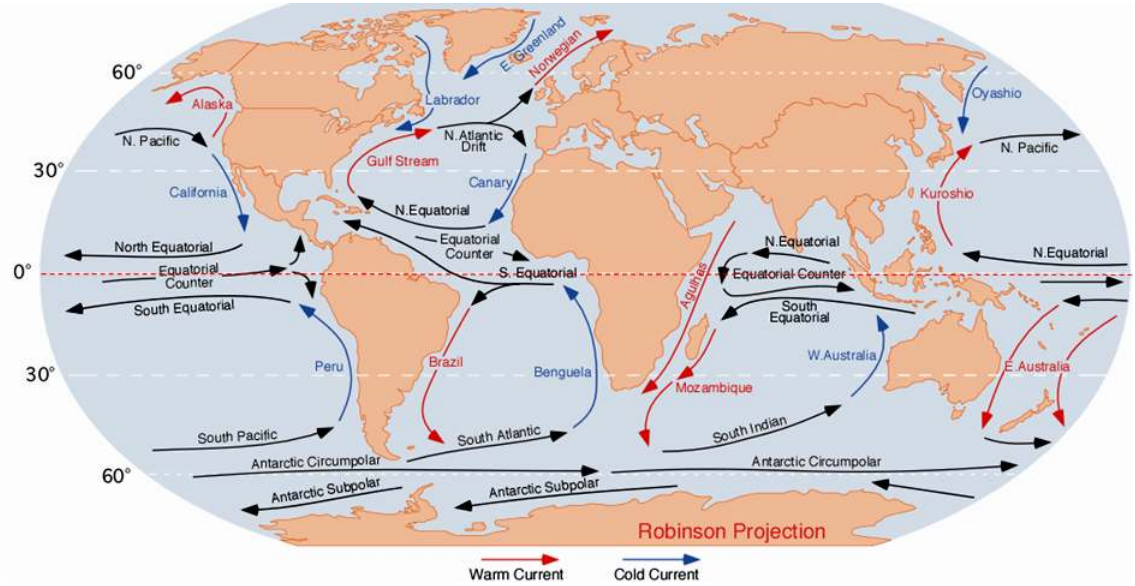


Figure 2.6.8: Overview of the main open-ocean currents. Red arrows represent warm water moving toward colder regions. Blue arrows represent cold water moving toward warmer regions. Black arrows represent currents that don't involve significant temperature changes.
Source: image "Corrientes Oceanicas" by Dr. Michael Pidwirny is available in the public domain.

Because the ocean basins are not like bathroom basins, not all ocean currents behave the way we would expect. In the North Pacific, for example, the main current flows clockwise, but there is a secondary current in the area adjacent to our coast—the Alaska Current—that flows counter-clockwise, bringing relatively warm water from California, past Oregon, Washington, and B.C. to Alaska. On Canada's eastern coast, the cold Labrador Current flows south past Newfoundland, bringing a stream of icebergs past the harbour at St. John's (Figure 2.6.9). This current helps to deflect the Gulf Stream toward the northeast, ensuring that Newfoundland stays cool, and western Europe stays warm.



Figure 2.6.9: An iceberg floating past Exploits Island on the Labrador Current.
Source: image "Newfoundland Iceberg" by Shawn is licensed under CC BY-SA 2.0.

The currents shown in Figure 2.6.8 are all surface currents, and they only involve the upper few hundred meters of the oceans. But there is much more going on underneath. The Gulf Stream, for example, which is warm and saline, flows past Britain and Iceland into the Norwegian Sea (where it becomes the Norwegian Current). As it cools down, it becomes denser, and because of its high salinity, which also contributes to its density, it starts to sink beneath the surrounding water (Figure 2.6.10). At this point, it is

known as **North Atlantic Deep Water** (NADW), and it flows to significant depth in the Atlantic as it heads back south. Meanwhile, at the southern extreme of the Atlantic, very cold water adjacent to Antarctica also sinks to the bottom to become **Antarctic Bottom Water** (AABW) which flows to the north, underneath the NADW.

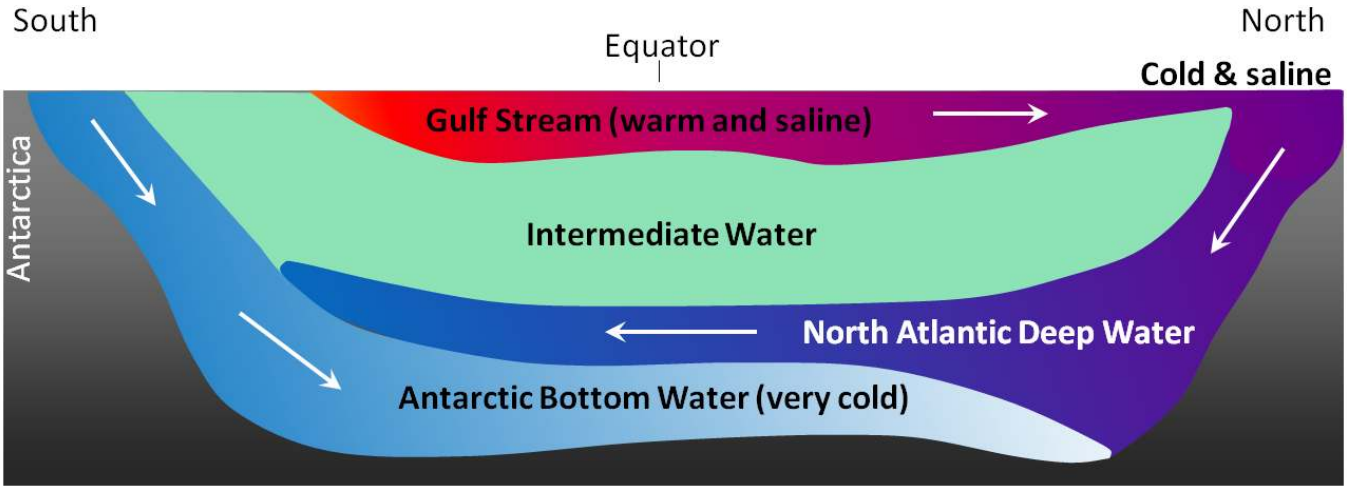


Figure 2.6.10: A depiction of the vertical movement of water along a north-south cross-section through the Atlantic basin. *Source: Steven Earle, licensed under CC BY.*

The descent of the dense NADW is just one part of a global system of seawater circulation, both at surface and at depth, as illustrated in Figure 2.6.11). The water that sinks in the areas of deep water formation in the Norwegian Sea and adjacent to Antarctica moves very slowly at depth. It eventually resurfaces in the Indian Ocean between Africa and India, and in the Pacific Ocean, north of the equator.

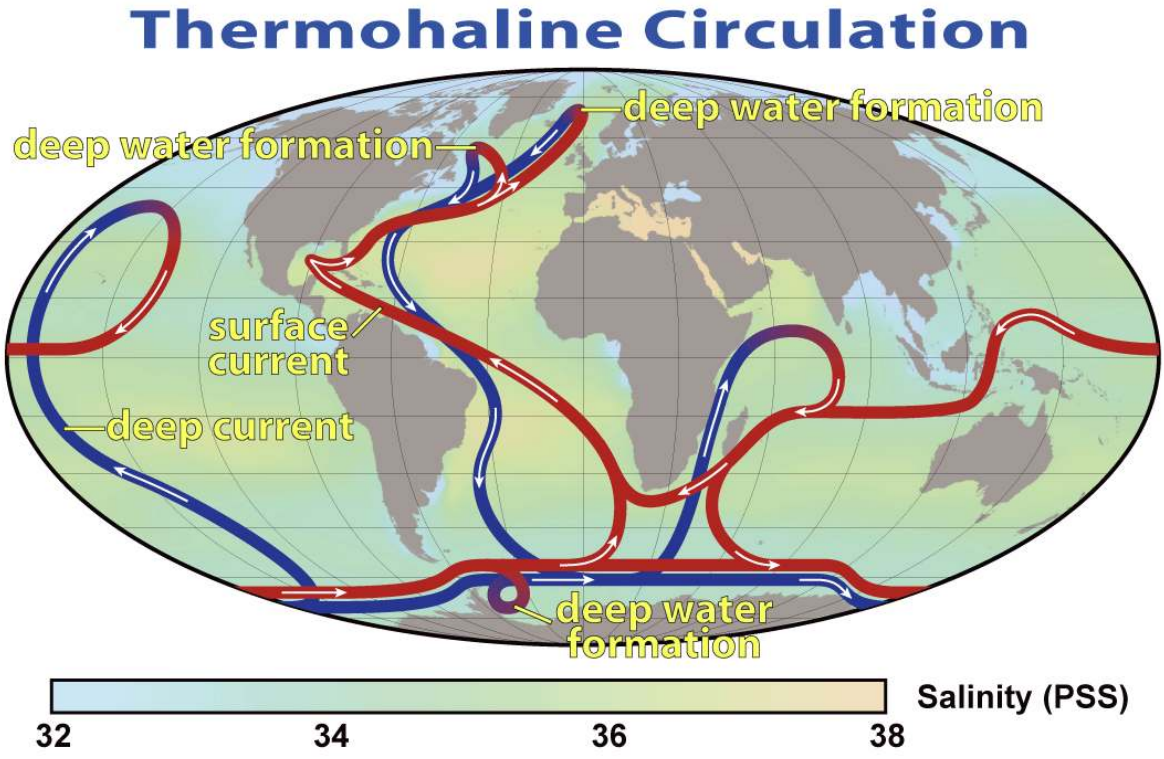


Figure 2.6.11: The thermohaline circulation system, also known as the Global Ocean Conveyor. *Source: image "A summary of the path of thermohaline circulation" by NASA is available in the public domain.*

The thermohaline circulation is critically important to the transfer of heat on Earth. It brings warm water from the tropics to the poles, and cold water from the poles to the tropics, thus keeping polar regions from getting too cold and tropical regions from getting too hot. A reduction in the rate of thermohaline circulation would lead to colder conditions and enhanced formation of sea ice at the poles. This would start a positive feedback process that could result in significant global cooling. There is compelling evidence to indicate that there were major changes in thermohaline circulation, corresponding with climate changes, during the Pleistocene Glaciation.

The movement of surface currents also plays a role in the vertical movements of deeper water, mixing the upper water column. **Upwelling** is the process that brings deeper water to the surface, and its major significance is that it brings nutrient-rich deep water to the nutrient-deprived surface, stimulating primary production (see section 7.3). **Downwelling** is where surface water is forced downwards, where it may deliver oxygen to deeper water. Downwelling leads to reduced productivity, as it extends the depth of the nutrient-limited layer. For more details on upwelling, downwelling, and ocean productivity see the section of Dr. Paul Webb's Oceanography book on Currents, Upwelling and Downwelling.

There are several interactions between ocean currents, ocean temperatures, and atmospheric circulation that cause cyclic global climate variability. The most well know of which is the **El Niño/Southern Oscillation** (**ENSO**) in the Pacific Ocean [also called **El Niño-La Niña Cycles**] associated with a band of warm ocean water that develops in the central and east-central equatorial Pacific. For more information on El Niño and La Niña, see the section of Dr. Paul Webb's Oceanography book on El Niño and La Niña. El Niño/Southern Oscillation (ENSO) is perhaps the most important ocean-atmosphere interaction phenomenon to cause cyclic global climate variability.

Contributors and Attributions

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2.7: What Makes the Climate Change

There are two parts to climate change, the first one is known as **climate forcing**, which is when conditions change to give the climate a little nudge in one direction or the other. The second part of climate change, and the one that typically does most of the work, is what we call a **feedback**. When a climate forcing changes the climate a little, a whole series of environmental changes take place, many of which either exaggerate the initial change (**positive feedbacks**), or suppress the change (**negative feedbacks**). In this section we will be discussing primarily natural climate forcing. Natural climate forcing has been going on throughout geological time. A wide range of processes has been operating at widely different time scales, from a few years to billions of years.

An example of a climate-forcing mechanism is the increase in the amount of carbon dioxide (CO_2) in the atmosphere that results from our use of fossil fuels. CO_2 traps heat in the atmosphere and leads to climate warming. Warming changes vegetation patterns; contributes to the melting of snow, ice, and permafrost; causes sea level to rise; reduces the solubility of CO_2 in sea water; and has a number of other minor effects. Most of these changes contribute to more warming. Melting of permafrost, for example, is a strong positive feedback because frozen soil contains trapped organic matter that is converted to CO_2 and methane (CH_4) when the soil thaws. Both these gases accumulate in the atmosphere and add to the warming effect. On the other hand, if warming causes more vegetation growth, that vegetation should absorb CO_2, thus reducing the warming effect, which would be a negative feedback. Under our current conditions—a planet that still has lots of glacial ice and permafrost—most of the feedbacks that result from a warming climate are positive feedbacks and so the climate changes that we cause get naturally amplified by natural processes.

Natural Climate Forcing

Life Cycle of the Sun

The longest-term natural forcing variation is related to the evolution of the Sun. Like most other stars of a similar mass, our Sun is evolving. For the past 4.57 billion years, its rate of nuclear fusion has been increasing, and it is now emitting about 40% more energy (as light) than it did at the beginning of geological time (Figure 2.7.1). A difference of 40% is big, so it's a little surprising that the temperature on Earth has remained at a reasonable and habitable temperature for all of this time. The mechanism for that relative climate stability has been the evolution of our atmosphere from one that was dominated by CO_2, and also had significant levels of CH_4—both GHGs—to one with only a few hundred parts per million of CO_2 and just under 1 part per million of CH_4 because, over geological time, life and its metabolic processes have evolved and changed the atmosphere.

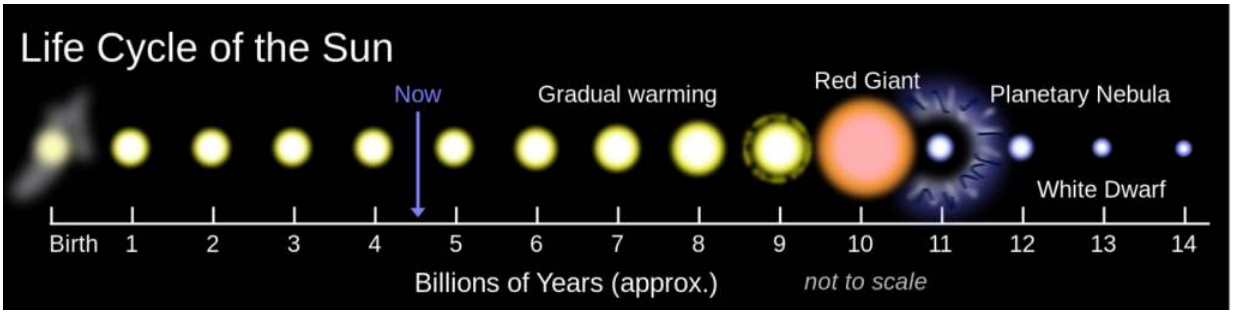


Figure 2.7.1**:** The life cycle of our Sun and of other similar stars. *Source: image "Solar Life Cycle" by Oliver Beatson is available in the public domain.*

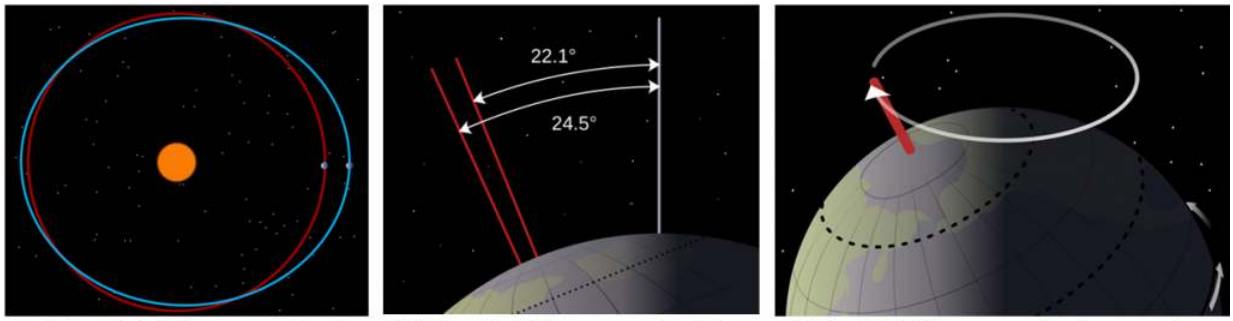
Changes occurring in the sun itself can affect the intensity of the sunlight that reaches Earth's surface. The intensity of the sunlight can cause either warming (during periods of stronger solar intensity) or cooling (during periods of weaker solar intensity). The sun follows a natural 11-year cycle of small ups and downs in intensity, but the effect of these 11-year cycles on Earth's climate is small.

Milankovitch Cycles

Earth's orbit around the Sun is nearly circular, but like all physical systems, it has natural oscillations (Figure 2.7.2). The importance of changes in the **eccentricity** (shape) of the Earth's orbit, **tilt** of the Earth, and **precession** (where the Earth's axis points) to Earth's climate cycles (now known as **Milankovitch Cycles**) was first pointed out by Yugoslavian engineer and

mathematician Milutin Milankovitch in the early 1900s. Milankovitch recognized that although the variations in the orbital cycles did not affect the total amount of **insolation** (light energy from the Sun) that Earth received, *it did affect where on Earth that energy was strongest*. Glaciations are most sensitive to the insolation received at latitudes of around 65°, and with the current configuration of continents, it would have to be 65° north (because there is almost no land at 65° south).

First, the shape of the orbit changes on a regular time scale — close to 100,000 years — from being close to circular to being very slightly elliptical. But the circularity of the orbit is not what matters; it is the fact that as the orbit becomes more elliptical, the position of the Sun within that ellipse becomes less central or more eccentric (Figure 2.7.2a). **Eccentricity** is important because when it is high, the Earth-Sun distance varies more from season to season than it does when eccentricity is low.



(a) The 100,000 year cycle of eccentricity of the Sun within the Earth's orbit. The blue orbit is more elliptical than the red one, and the Sun is offset from the centre of the ellipse

(b) The 41,000 year cycle of the angle of tilt (obliquity) of the Earth's axis (red lines) compared to a line perpendicular to the plane of the Earth's orbit (light blue line).

(c) the 20,000 year cycle of precession of the Earth's rotational axis

Figure 2.7.2: The cycles of Earth's orbit and rotation. These are also called the Milankovitch Cycles. *Source: Steven Earle, licensed under CC BY.*

Second, Earth rotates around an axis through the North and South Poles, and that axis is at an angle to the plane of Earth's orbit around the Sun (Figure 2.7.2b). The angle of tilt (also known as **obliquity**) varies on a time scale of 41,000 years. When the angle is at its maximum (24.5°), Earth's seasonal differences are accentuated. When the angle is at its minimum (22.1°), seasonal differences are minimized. The current hypothesis is that glaciation is favored at low seasonal differences as summers would be cooler and snow would be less likely to melt and more likely to accumulate from year to year.

Third, the direction in which Earth's rotational axis points also varies, on a time scale of about 20,000 years (Figure 2.7.2c). This variation, known as **precession**, means that although the North Pole is presently pointing to the star Polaris (the pole star), in 10,000 years it will point to the star Vega.

The most important aspects are whether the northern hemisphere is pointing toward the Sun at its closest or farthest approach, and how eccentric the Sun's position is in Earth's orbit. Two opposing situations are when the northern hemisphere is at its farthest distance from the Sun during summer, which means cooler summers, and when the northern hemisphere is at its closest distance to the Sun during summer, which means hotter summers. Cool summers—as opposed to cold winters—are the key factor in the accumulation of glacial ice, so the scenario where the northern hemisphere is at its farthest distance from the Sun during summer is the one that promotes glaciation. This factor is greatest when eccentricity is high (so the difference between the closest point to the Sun and furthest point from the Sun is larger). For a more detailed explanation on Mikankovich Cycles see Milankovitch.

As already stated, **climate feedbacks** are critically important in amplifying weak climate forcings into full-blown climate changes. When Milankovitch published his hypothesis in 1924, it was widely ignored, partly because it was evident to climate scientists that the forcing produced by the orbital variations was not strong enough to drive the significant climate changes of the glacial cycles. Those scientists did not recognize the power of positive feedbacks. It was not until 1973, 15 years after Milankovitch's death, that sufficiently high-resolution data were available to show that the Pleistocene glaciations were indeed driven by the orbital cycles, and it became evident that the orbital cycles were just the forcing that initiated a range of feedback mechanisms that made the climate change.

Data for tilt, eccentricity, and precession over the past 400,000 years have been used to determine the insolation levels at 65° north, as shown in Figure 2.7.4. Also shown in Figure 2.7.4 are Antarctic ice-core temperatures from the same time period. The correlation between the two is clear, and it shows up in the Antarctic record because when insolation changes lead to growth of glaciers in the northern hemisphere, southern-hemisphere temperatures are also affected.

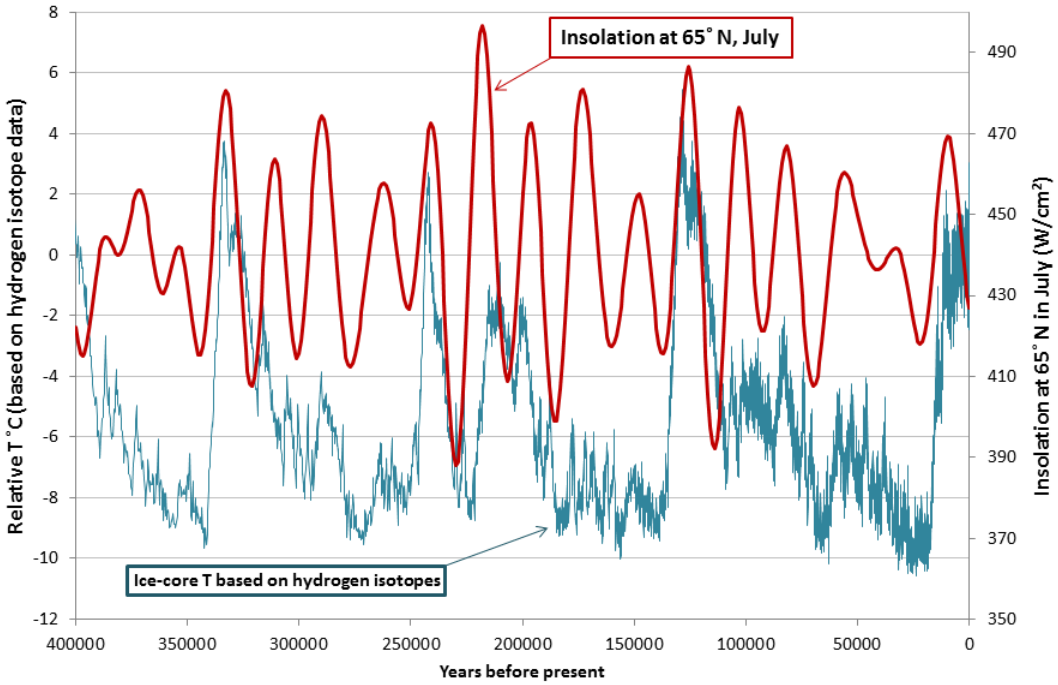


Figure 2.7.4: Insolation at 65° N in July compared with Antarctic ice-core temperatures.
Source: Steven Earle, licensed under CC BY. Based on data from Valerie Masson-Delmotte, "EPICA Dome C Ice Core 800KYr Deuterium Data and Temperature Estimates," WDCA Contribution Series Number : 2007 -091, NOAA/NCDC Paleoclimatology Program, Boulder CO, USA. Retrieved from: NOAA and from Berger, A. and Loutre, M.F. (1991). Insolation values for the climate of the last 10 million years. Quaternary Science Reviews, 10, 297-317.

Plate Tectonic Processes

Plate tectonic processes contribute to climate forcing in several different ways, and on time scales ranging from tens of millions to hundreds of millions of years. One mechanism is related to continental position. For example, we know that Gondwana (South America + Africa + Antarctica + Australia) was positioned over the South Pole between about 450 and 250 Ma, during which time there were two major glaciations (Andean-Saharan and Karoo) affecting the South polar regions and cooling the rest of the planet at the same time. Another mechanism is related to continental collisions. For example, the collision between India and Asia, which started at around 50 Ma, resulted in massive tectonic uplift. The consequent accelerated weathering of this rugged terrain consumed CO_2 from the atmosphere and contributed to gradual cooling over the remainder of the Cenozoic. Changes in continental position can also lead to changes in ocean circulation, and therefore the distribution of energy from equator to the poles. For example, the opening of the Drake Passage — due to plate-tectonic separation of South America from Antarctica — led to the development of the Antarctic Circumpolar Current, which isolated Antarctica from the warmer water in the rest of the ocean and thus contributed to Antarctic glaciation starting at around 35 Ma.

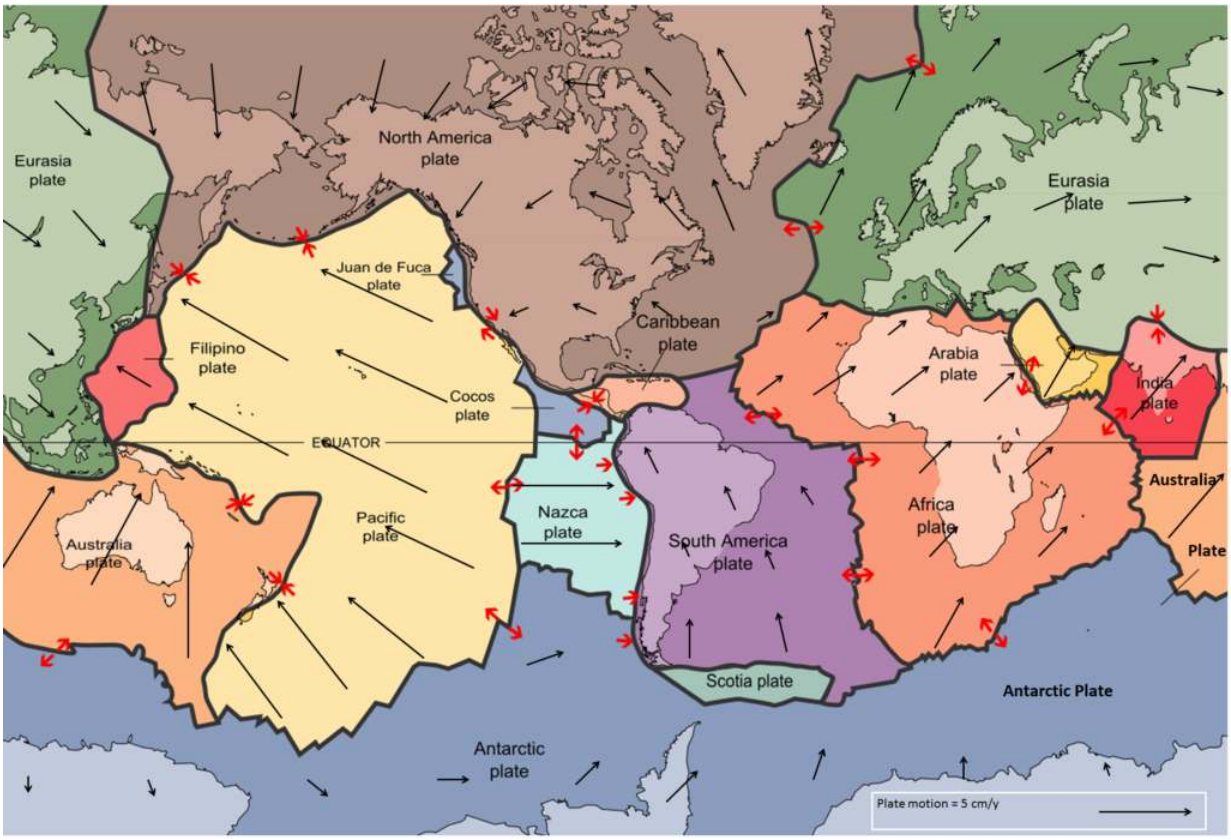


Figure 2.7.5**:** A map showing 15 of the Earth's tectonic plates and the approximate rates and directions of plate motions. *Source: image "Tectonic Plates" by USGS is available in the public domain and was adapted by Steven Earle.*

Volcanic eruptions don't just involve lava flows and exploding rock fragments; various particulates and gases are also released, including carbon dioxide, water vapor, sulfur dioxide, hydrogen sulfide, hydrogen, and carbon monoxide. Volcanic eruptions can last a few days, but the solids and gases released during an eruption can influence the climate over a period of a few years, causing short-term climate changes. Generally, volcanic eruptions cool the climate. Sulphur dioxide is an aerosol that reflects incoming solar radiation and has a net cooling effect that is short-lived (a few years in most cases, as the particulates settle out of the atmosphere within a couple of years), and doesn't typically contribute to longer-term climate change. This occurred in 1783 when volcanoes in Iceland erupted and caused the release of large volumes of sulfuric oxide. This led to haze-effect cooling, a global phenomenon that occurs when dust, ash, or other suspended particles block out sunlight and trigger lower global temperatures as a result; haze-effect cooling usually extends for one or more years. In Europe and North America, haze-effect cooling produced some of the lowest average winter temperatures on record in 1783 and 1784. Volcanic CO_2 emissions can contribute to climate warming but only if a greater-than-average level of volcanism is sustained over a long time (at least tens of thousands of years). It is widely believed that the catastrophic end-Permian extinction (at 250 Ma) resulted from warming initiated by the eruption of the massive Siberian Traps over a period of at least a million years.

Greenhouse Gas Concentrations

Since scientists cannot go back in time to directly measure climatic variables, such as average temperature and precipitation, they must instead indirectly measure temperature. Antarctic ice cores are a key example of such evidence. These ice cores are samples of polar ice obtained by means of drills that reach thousands of meters into ice sheets or high mountain glaciers. Viewing the ice cores is like traveling backwards through time; the deeper the sample, the earlier the time period. Trapped within the ice are bubbles of air and other biological evidence that can reveal temperature and carbon dioxide data. Antarctic ice cores have been collected and analyzed to indirectly estimate the temperature of the Earth over the past 400,000 years (Figure 2.7.6a). The 0 °C on this graph refers to the long-term average. Temperatures that are greater than 0 °C exceed Earth's long-term average temperature.

Conversely, temperatures that are less than 0 °C are less than Earth's average temperature. This figure shows that there have been periodic cycles of increasing and decreasing temperature.

Before the late 1800s, the Earth has been as much as 9 °C cooler and about 3 °C warmer. Note that the graph in Figure 2.7.6b shows that the atmospheric concentration of carbon dioxide has also risen and fallen in periodic cycles; note the relationship between carbon dioxide concentration and temperature. Figure 2.7.6b shows that carbon dioxide levels in the atmosphere have historically cycled between 180 and 300 parts per million (ppm) by volume.

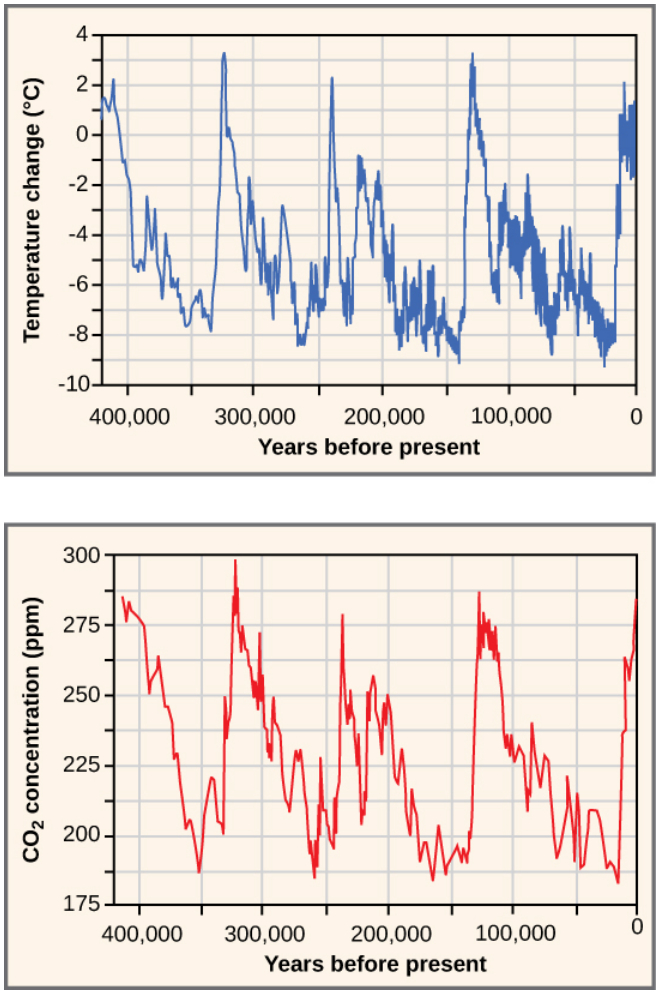


Figure 2.7.6: Ice at the Russian Vostok station in East Antarctica was laid down over the course 420,000 years and reached a depth of over 3,000 m. By measuring the amount of CO_2 trapped in the ice, scientists have determined past atmospheric CO_2 concentrations. Temperatures relative to modern day were determined from the amount of deuterium (an isotope of hydrogen) present.

Changes in Ocean Currents

Ocean currents are important to climate, and currents also have a tendency to oscillate. Glacial ice cores show clear evidence of changes in the Gulf Stream (and other parts of the thermohaline circulation system) that affected global climate on a time scale of about 1,500 years during the last glaciation.

The east-west changes in sea-surface temperature and surface pressure in the equatorial Pacific Ocean—known as the El Niño Southern Oscillation or ENSO—varies on a much shorter time scale of between two and seven years. These variations tend to garner the attention of the public because they have significant climate implications in many parts of the world. The past 65 years of ENSO index values are shown in Figure 2.7.7. The strongest **El Niños** in recent decades were in 1983 and 1998, and those were

both very warm years from a global perspective. During a strong El Niño, the equatorial Pacific sea-surface temperatures are warmer than normal and heat the atmosphere above the ocean, which leads to warmer-than-average global temperatures.

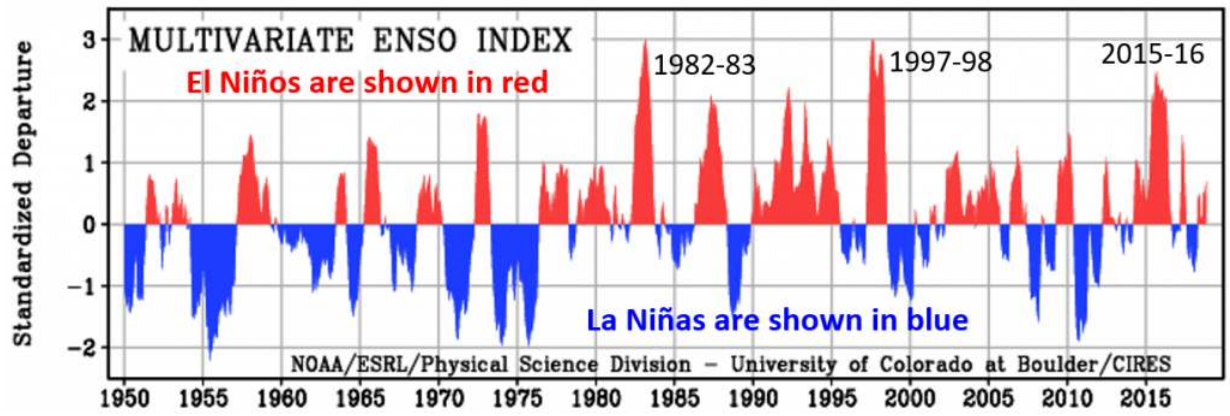


Figure 2.7.7: Variations in the ENSO index from 1950 to early-2019. *Source: Steven Earle with NOAA ("Multivariate ENSO Index (MEI)."*

For more information on El Niño and La Niña, see the section of Dr. Paul Webb's Oceanography book on El Niño and La Niña.

Contributors and Attributions

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2.8: Past Climate Change

Over Earth's history, the climate has changed a lot. For example, during the Mesozoic Era, the Age of Dinosaurs, the climate was much warmer and carbon dioxide was abundant in the atmosphere. However, throughout the Cenozoic Era (65 Million years ago to today), the climate has been gradually cooling. This section summarizes some of these major past climate changes.

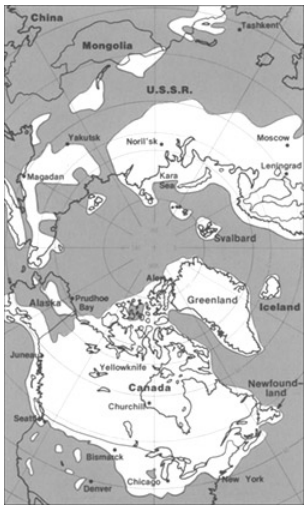


Figure 2.8.1: Maximum extent of Laurentide Ice Sheet.

Past Glaciations

Through geologic history, the climate has changed slowly over millions of years. Before the most recent Pliocene-Quaternary glaciation (Figure 2.8.1), there were three other major glaciations (Deynoux et al., 2004). The oldest, known as the Huronian, occurred toward the end of the Archean-early Proterozoic (~2.5 billion years ago). The major event of that time, the great oxygenation event, is most commonly associated with the cause of that glaciation. The increased oxygen is thought to have reacted with the potent greenhouse gas methane, causing cooling (Kopp et al., 2005).

The end of the Proterozoic (about 700 million years ago) had another glaciation, known as the **Snowball Earth hypothesis** (Hoffman et al., 1998). Glacial evidence has been interpreted in widespread rock sequences globally and even has been linked to low-latitude glaciation (Schopf & Klein, 1992). Limestone rock (usually formed in tropical marine environments) and glacial deposits (usually formed in cold climates) are often found together from this time in regions all around the world. In Utah, Antelope Island in the Great Salt Lake has interbedded limestone and glacial deposits (diamictites) interpreted to be formed by continental glaciation (Doelling et al., 1988). The idea of the controversial Snowball Earth hypothesis is that a runaway albedo effect (ice and snow reflecting solar radiation) might cause the complete freezing of land and ocean surfaces and a collapse of biological activity. The ice-covered earth would only melt when carbon dioxide from volcanoes reached high concentrations, due to the inability for carbon dioxide to enter the then-frozen ocean. Some studies estimated carbon dioxide was 350 times higher than today’s concentrations (Hoffman et al., 1998). The complete freezing and the extent of the freezing has come into question (Allen & Etienne, 2008; Eyles & Januszczak, 2004).

Glaciation also occurred in the Paleozoic, most notably with the Karoo Glaciation of the Pennsylvanian (323 to 300 million years ago). This also was caused by an increase of oxygen and a subsequent drop in carbon dioxide, most likely produced by the evolution and rise of land plants (Berner, 1998).

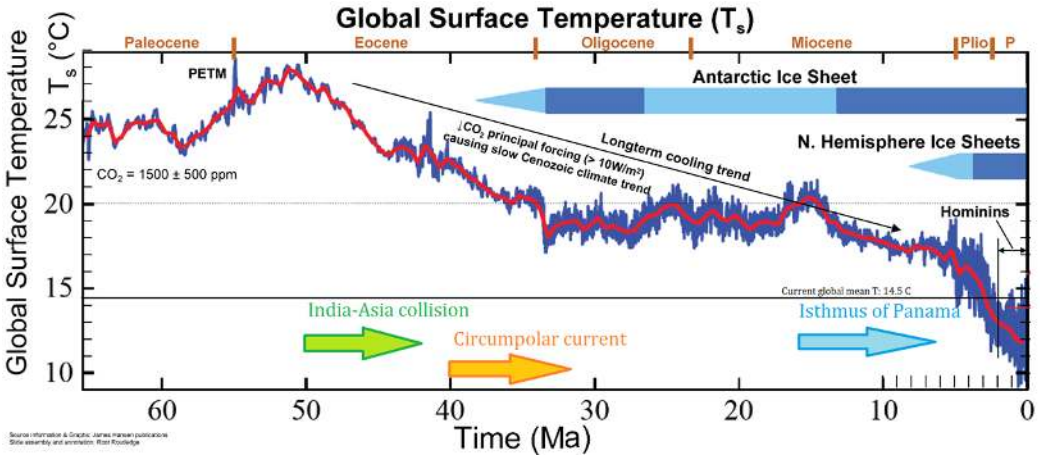


Figure 2.8.2: Global average surface temperature over the past 70 million years.

During the Cenozoic Era (the last 65 million years), the climate started out warm and gradually cooled to today. This warm time is called the **Paleocene-Eocene Thermal Maximum** and Antarctica and Greenland were ice-free during this time (Figure 2.8.2). Since the Eocene, tectonic events during the Cenozoic caused persistent and significant planetary cooling. For example, the collision of the Indian Plate with the Asian Plate created the Himalaya Mountains increasing weathering and erosion rates. An increased rate of weathering of silicate minerals, especially feldspar, consumes carbon dioxide from the atmosphere and therefore reduces the greenhouse effect, resulting in long-term cooling (Kump et al., 2000).

At about 40 Ma, the narrow gap between the South American Plate and the Antarctica Plate widened, resulting in the opening of the Drake Passage. This allowed for the unrestricted west-to-east flow of water around Antarctica, the Antarctic Circumpolar Current, which effectively isolated the southern ocean from the warmer waters of the Pacific, Atlantic, and Indian Oceans (Figure 2.8.3). The region cooled significantly, and by 35-million-year ago (Oligocene) glaciers had started to form on Antarctica (Lagabrielle et al., 2009).

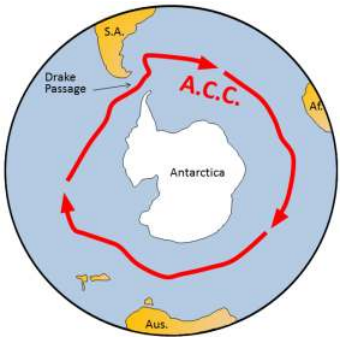
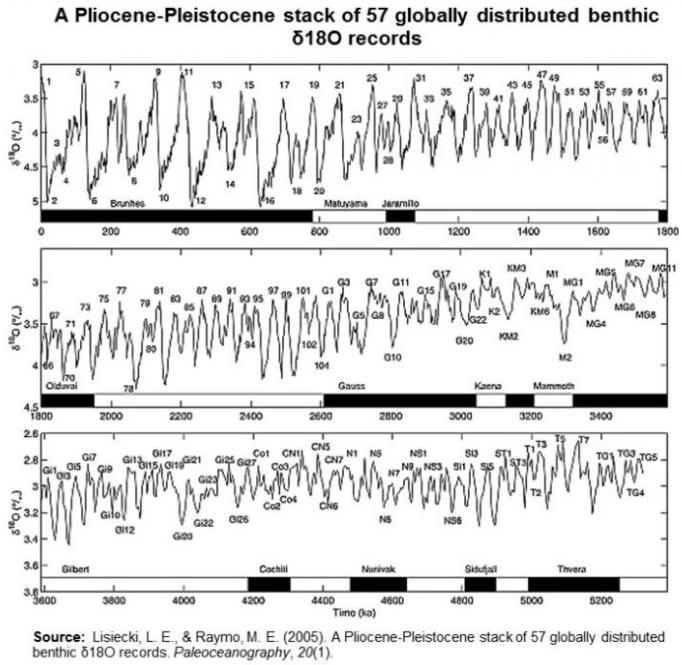


Figure 2.8.3: The Antarctic Circumpolar Current.

At around 15 Ma, subduction-related volcanism between Central and South America created the Isthmus of Panama that connected North and South America. This prevented water from flowing between the Pacific and Atlantic Oceans and reduced heat transfer from the tropics to the poles. This created a cooler Antarctica and larger Antarctic glaciers. The expansion of that ice sheet (on land and water) increased Earth's reflectivity (albedo), a positive feedback loop of further cooling: more reflective glacial ice, more cooling, more ice, and so on (Kuipers Munneke et al., 2011; Curry et al., 1995).

By 5 million years ago (Pliocene Epoch), ice sheets had started to grow in North America and northern Europe. The most intense part of the current glaciation is the last 1 million years of the Pleistocene Epoch. The Pleistocene has significant temperature variations (through a range of almost 10°C) on time scales of 40,000 to 100,000 years, and corresponding expansion and contraction of ice sheets. These variations are attributed to subtle changes in Earth's orbital parameters called **Milankovitch cycles**, which are explained in more detail in the section on natural climate forcings (Milankovitch, 1930; Roe, 2006). Over the past

million years, the glaciation cycles have been approximately every 100,000 years with many glacial advances in the last 2 million years (Figure 2.8.4) (Abe-Ouchi et al., 2013; Lisiecki and Raymo, 2005).



Source: Lisiecki, L. E., & Raymo, M. E. (2005). A Pliocene-Pleistocene stack of 57 globally distributed benthic δ18O records. *Paleoceanography*, *20*(1).

Figure 2.8.4: A Pliocene-Pleistocene stack of 57 globally distributed benthic δ18O records. X-axis is time in thousands of years (ka) so 200 is actually 200,000. *Source: Lisiecki and Raymo, 2005.*

Warmer portions of climate within an ice age are called **interglacials**, with brief versions called **interstadials**. These warming upticks are related to variations in Earth's climate like Milankovitch cycles. In the last 500,000 years, there have been 5 or 6 interglacials, with the most recent belonging to our current time, the Holocene (Figure 2.8.4).

Two of the more recent climate swings demonstrate the complexity of the changes: the Younger Dryas and the Holocene Climatic Optimum. These events are more recent and yet have conflicting information. The Younger Dryas cooling is widely recognized in the Northern Hemisphere, though the timing of the event (about 12,000 years ago) does not appear to be equal everywhere (Carlson, 2013; Fairbanks, 1990). It also is difficult to find in the Southern Hemisphere (Kaplan et al., 2010). The Holocene Climatic Optimum is the warming around 6,000 years ago, though it was not universally warmer, and probably not as warm as current warming, and not at the same time everywhere (Ganopolski et al., 1998; Hewitt & Mitchell, 1998; He et al., 2004).

Two significant temperature anomalies, or irregularities, have occurred in the last 2000 years. These are the Medieval Climate Anomaly (or the Medieval Warm Period) and the Little Ice Age. A third temperature anomaly aligns with the Industrial Era. The Medieval Climate Anomaly occurred between 900 and 1300 AD. During this time period, many climate scientists think that slightly warmer weather conditions prevailed in many parts of the world; the higher-than-average temperature changes varied between 0.10 °C and 0.20 °C above the norm. Although 0.10 °C does not seem large enough to produce any noticeable change, it did free seas of ice. Because of this warming, the Vikings were able to colonize Greenland. The Little Ice Age was a cold period that occurred between 1550 AD and 1850 AD. During this time, a slight cooling of a little less than 1 °C was observed in North America, Europe, and possibly other areas of the Earth. This 1 °C change in global temperature is a seemingly small deviation in temperature (as was observed during the Medieval Climate Anomaly); however, it also resulted in noticeable changes. Historical accounts reveal a time of exceptionally harsh winters with much snow and frost.

Proxy Indicators of Past Climates

How do we know about past climates? Scientists use proxy indicators to understand past climate. A **proxy indicator** is a biological, chemical, or physical signature preserved in the rock, sediment, or ice record that acts like a "fingerprint" of something in the past (Weissert, 2000). Thus they are an indirect indicator of something like climate. For ancient glaciations from the Proterozoic and Paleozoic, there are rock formations of glacial sediments such as the diamictite (or tillite) of the Mineral Fork Formation in Utah. This dark rock has many fine-grained components plus some large out-sized clasts like a modern glacial till (Ojakangas & Matsch, 1980; Christie-Blick et al., 1982).

For climate changes during the Cenozoic Era (the last 65 Ma), there is a detailed chemical record from the coring of deep-sea sediments as part of the Ocean Drilling Program (Figure 2.8.5). Studies of deep-sea sediment use stable carbon and oxygen isotopes obtained from the shells of deep-sea benthic foraminifera that have settled on the ocean floor over millions of years. Oxygen isotopes are a proxy indicator of deep-sea temperatures and continental ice volume (Zachos et al., 2001).

Sediment Cores – Stable Oxygen Isotope



Figure 2.8.5: Sediment core from the Greenland continental slope. *Source: Hannes Grobe.*

Oxygen isotopes are an indicator of past climate. The two main stable oxygen isotopes are ^{16}O and ^{18}O. They both occur in water (H_2O) and in the calcium carbonate ($CaCO_3$) shells of foraminifera as the oxygen component of both of those molecules. The most abundant and lighter isotope is ^{16}O. Since it is lighter, it evaporates more easily from the ocean's surface as water vapor, which later turns to clouds and precipitation on the ocean and land.

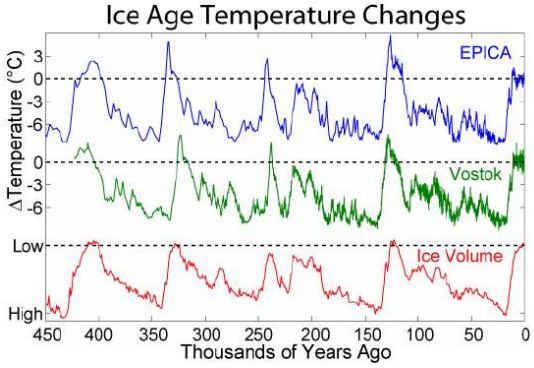


Figure 2.8.6: Antarctic temperature changes during the last few glaciations compared to global ice volume. The first two curves are based on the deuterium (heavy hydrogen) record from ice cores (EPICA Community Members 2004, Petit et al. 1999). The bottom line is ice volume based on oxygen isotopes from a composite of deep-sea sediment cores (Lisiecki and Raymo 2005).

During geologic times when the climate is cooler, more of this precipitation is locked onto land in the form of glacial ice. Consider the giant ice sheets, more than a mile thick, that covered a large part of North America during the last ice age only 14,000 years ago. During glaciation, the glaciers effectively lock away more ^{16}O, thus the ocean water and foraminifera shells become enriched in ^{18}O. Therefore, a ratio of ^{18}O to ^{16}O in calcium carbonate shells of foraminifera is an indicator of past climate. The sediment cores from the Ocean Drilling Program record a continuous accumulation of sediment (Figure 2.8.6).

Sediment Cores – Boron Isotopes and Acidity

Boron-isotope ratios in ancient planktonic foraminifera shells in deep-sea sediment cores have been used to estimate the pH (acidity) of the ocean over the past 60 million years. Ocean acidity is a proxy for past atmospheric CO^2 concentrations. In the early Cenozoic, around 60 million years ago, CO^2 concentrations were over 2,000 ppm and started falling around 55 to 40 million years ago possibly due to reduced CO^2 outgassing from ocean ridges, volcanoes, and metamorphic belts and increased carbon burial due to uplift of the Himalaya Mountains. By the Miocene (about 24 million years ago), CO^2 levels were below 500 ppm and by 800,000 years ago CO^2 levels didn't exceed 300 ppm (Pearson & Palmer, 2000; Lüthi et al., 2008).

Carbon Dioxide Concentrations in Ice Cores

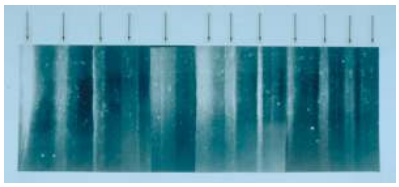


Figure 2.8.7: 19 cm long section of ice core showing 11 annual layers with summer layers (arrowed) sandwiched between darker winter layers. *Source: US Army Corps of Engineers.*

For the more recent Pleistocene climate, there is a more detailed and direct chemical record from coring into the Antarctic and Greenland ice sheets (Figure 2.8.7). Snow accumulates on these ice sheets and creates yearly layers. Ice cores have been extracted from ice sheets covering the last 800,000 years. Oxygen isotopes are collected from these annual layers and the ratio of ^{18}O to ^{16}O is used to determine temperature as discussed above. In addition, the ice traps small atmospheric gas bubbles as the snow turns to ice.

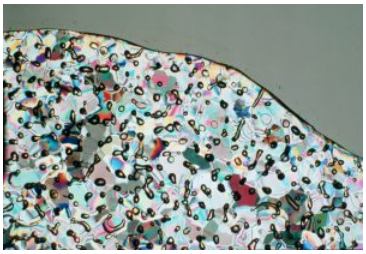


Figure 2.8.8**:** Antarctic ice showing hundreds of tiny trapped air bubbles from the atmosphere thousands of years ago. *Source: CSIRO.*

Small pieces of this ice are crushed and the ancient air extracted into a mass spectrometer that can detect the chemistry of the ancient atmosphere. Carbon dioxide levels are recreated from these measurements. Over the last 800,000 years, the maximum carbon dioxide concentration during warm times was about 300 ppm and the minimum during cold stretches was about 170 ppm (Pearson & Palmer, 2000; Lüthi et al., 2008; Oak Ridge National Laboratory, 2008) (Figure 2.8.9). The carbon dioxide content of earth's atmosphere is currently over 400 ppm.

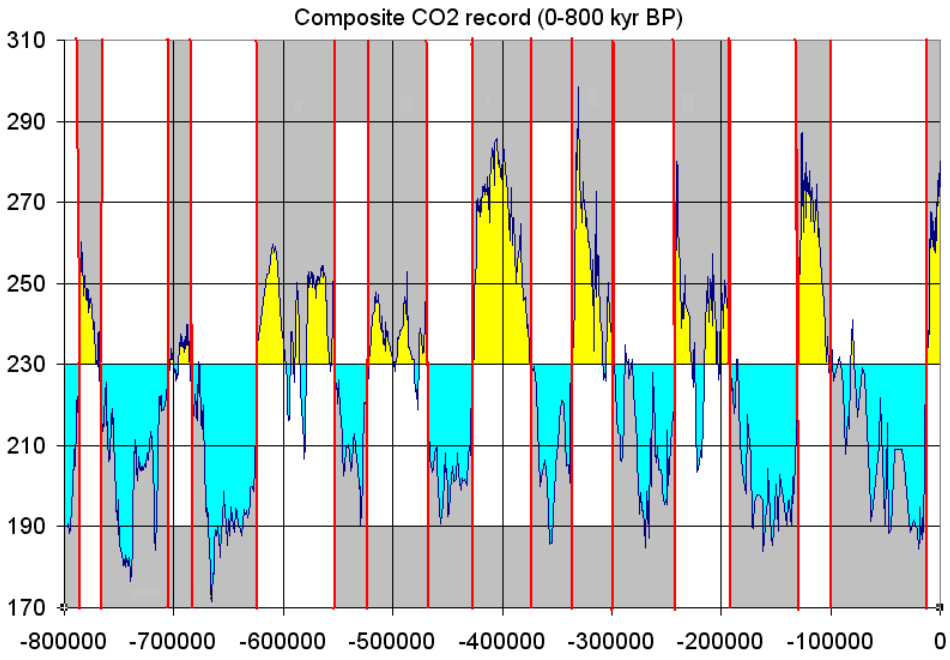


Figure 2.8.9: Composite carbon dioxide record from the last 800,000 years based on ice core data from EPICA Dome C Ice Core.

Oceanic Microfossils

Microfossils, like foraminifera, diatoms, and radiolarians, can be used to interpret past climate records. In sediment cores, different species of microfossils are found in different layers. Groups of these microfossils are called assemblages. One assemblage consists of species that lived in cooler ocean water (in glacial times) and another assemblage found at a different level in the same sediment core is made of warmer water species (Cunningham et al., 1999).





Tree Rings

Every year a tree will grow one ring with a light section and dark section (Figure 2.8.10). The rings vary in width. Since trees need a lot of water to survive, narrower rings indicate colder and drier climates. Since some trees can be several thousands years old, we can use their rings for regional paleoclimatic reconstructions. Further, dead trees such as those used in Puebloan ruins can be used to extend this proxy indicator, which showed long term droughts in the region and why their villages were abandoned (Figure 2.8.11).



Figure 2.8.10: Tree rings form every year. Rings that are farther apart are from wetter years and rings that are closer together are from dryer years.

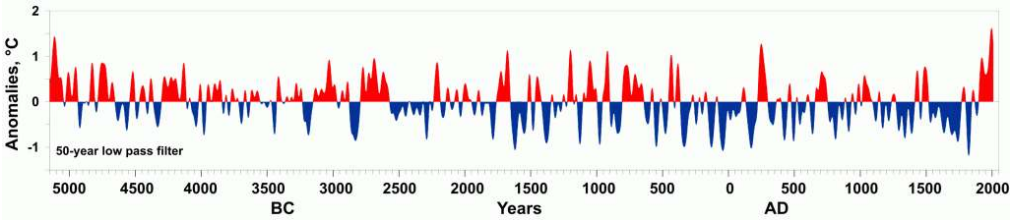


Figure 2.8.11**:** Summer temperature anomalies for the past 7000 years. *Source: R.M.Hantemirov.*

Pollen

Flowering plants produce pollen grains. Pollen is distinctive when viewed under a microscope (Figure 2.8.12). Sometimes pollen can be preserved in lake sediments that accumulate every year. Coring of lake sediments can reveal ancient pollen. Fossil pollen assemblages are groups of pollen from multiple species such as spruce, pine, and oak. Through time (via the sediment cores and radiometric age-dating techniques), the pollen assemblage will change revealing the plants that lived in the area at the time. Thus the pollen assemblages are an indicator of past climate since different plants will prefer different climates (Webb & Thompson, 1986). For example, in the Pacific Northwest east of the Cascades, a region close to the border of grasslands and forest, a study tracked pollen over the last 125,000 years covering the last two glaciations. As shown in the figure (Fig. 2 from reference Whitlock and Bartlein, 1997), pollen assemblages with more pine tree pollen are found during glaciations and pollen assemblages with less pine tree pollen are found during interglacial times (Whitlock & Bartlein, 1997).

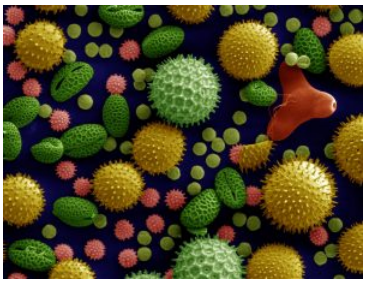


Figure 2.8.12**:** Scanning electron microscope image of modern pollen with false color added to distinguish plant species. *Source: Dartmouth Electron Microscope Facility, Dartmouth College.*

Other Proxy Indicators

Paleoclimatologists study many other phenomena to understand past climates such as human historical accounts, human instrument record from the recent past, lake sediments, cave deposits of calcium carbonates, and corals (both oxygen isotopes and growth rings).

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CHAPTER OVERVIEW

Chapter 3: Evolution - History, Evidence, and Mechanisms

Learning Objectives

- Explain evolution as an underlying theme in biology
- Describe adaptations as a general concept
- Describe the wide range of adaptations of individual species use to interact with and adjust to variations in their environment
- Discuss misconceptions about the theory of evolution
- Identify the major requirements of natural selection
- Explain the relationships among adaptation, natural selection, and evolution
- Compare and contrast additional mechanisms of evolution: mutation, genetic drift, and gene flow.

3.1: Understanding Evolution

3.2: Evidence of Evolution

3.2.1: Scientist Spotlight - Ynes Enriquetta Julietta Mexia

3.3: Natural Selection and Adaptive Evolution

3.4: Additional Mechanisms of Evolution

Cover photo: "Dinosaur footprint" (Greg Willis, CC BY-SA 2.0)

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3.1: Understanding Evolution

Understanding Evolution

- Please read and watch the following Mandatory Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 2 hours.
- Optional Activities are embedded.
- To navigate to the next Section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Describe the historical influences on Darwin's and Wallace's theory of evolution
- Explain the requirements of evolution.
- Identify the major misconceptions of evolution and why they are incorrect.

Introduction: Evolution

Video





This 12-minute video summarizes much of the material below. You may want to revisit this video at the end of the Unit.

Question after watching: Darwin famously wrote that "endless forms most beautiful have been and are being evolved." In what way do we know that evolution is still taking place today?

The theory of evolution is the unifying theory of biology, meaning it is the framework within which biologists ask questions about the living world. The Ukrainian-born American geneticist Theodosius Dobzhansky famously wrote in 1964 that "nothing makes sense in biology except in the light of evolution." [1] The tenet that all species have evolved and diversified from a common ancestor is the foundation from which we approach all questions in biology. It provides a direction for predictions about living things and has been validated through extensive scientific experimentation. **Evolution** is simply a change in the gene pool of a species over time. More technically, evolution is the change in genetic composition of a population over time, specifically over generations, resulting from differential survival and reproduction of individuals. Evolution by natural selection describes one mechanism for this change. Natural selection is introduced here but is discussed in further detail in Section 2.2.3. Additional mechanisms are discussed in Section 2.2.4.

Adaptations

A heritable trait that aids the survival and reproduction of an organism in its present environment is called an **adaptation**. A population is adapted when a change in the range of genetic variation occurs over time that increases or maintains the survivability of that population in its current environmental conditions. The webbed feet of platypuses are an adaptation for swimming. The snow leopards' thick fur is an adaptation to living in the cold. The cheetahs' fast speed is an adaptation for catching prey.



Figure 3.1.1: All organisms are products of evolution via adaptations to their environment. (a) Saguaro (*Carnegiea gigantea*) can soak up 750 liters of water in a single rain storm, enabling these cacti to survive the dry conditions of the Sonoran desert in Mexico and the Southwestern United States. (b) The Andean semiaquatic lizard (*Potamites montanicola*), discovered in Peru in 2010, lives between 1,570 to 2,100 meters in elevation and, unlike most lizards, is nocturnal and swims. Scientists still do not know how these cold-blood animals are able to move in the cold (10 to 15°C) temperatures of the Andean night.

Whether or not an individual trait is favorable depends on the environmental conditions at the time. The same traits are not always selected because environmental conditions can change. For example, consider a species of plant that grew in a moist climate and did not need to conserve water. Large leaves were selected because they allowed the plant to obtain more energy from the sun. Large leaves require more water to maintain than small leaves, and the moist environment provided favorable conditions to support large leaves. After thousands of years, the climate changed and the area no longer had excess water. The direction of natural selection shifted so that plants with small leaves were selected because those populations were able to conserve water to survive the new environmental conditions.

Video





This video identifies the three types of adaptations organisms may possess.
Questions after watching: What sorts of adaptations might you expect to arise in a plant species or a bacterial/unicellular species? Do you expect that the three types described in the video for animals will apply to these types of species?

History of the Theory of Evolution

Well before Darwin began to explore the concept of evolution, the idea that species change over time had already been suggested and debated. The view that species are static and unchanging was grounded in the writings of Plato more than 2000 years ago, yet there were also ancient Greeks who expressed ideas about evolution. During the eighteenth century, ideas about the evolution of animals were reintroduced by the naturalist Georges-Louis Leclerc Comte de Buffon who observed that various geographic regions have different plant and animal populations, even when the environments are similar. It was also accepted that there are extinct species.

During this time, a Scottish naturalist named James Hutton proposed that geological change occurs gradually by the accumulation of small changes over long periods of time. This theory contrasted with the predominant view of the time: that the geology of the planet is a consequence of catastrophic events that occurred during a relatively brief past. During the nineteenth century, Hutton's views were popularized by the geologist Charles Lyell, who was a friend of Charles Darwin. Lyell's ideas, in turn, influenced

Darwin's concept of evolution. The greater age of the earth proposed by Lyell supported the gradual evolution that Darwin proposed, and the slow process of geological change provided an analogy for the gradual change in species.

In the early nineteenth century, Jean-Baptiste Lamarck published a book that detailed a different mechanism for evolutionary change. This mechanism is now referred to as an inheritance of acquired characteristics. This idea states that modifications in an individual are caused by its environment, or the use or disuse of a structure during its lifetime. These changes can be inherited by its offspring, bringing about change in a species. While this mechanism for evolutionary change is now known to be incorrect, Lamarck's ideas were an important influence on the initial concepts of evolution.

Charles Darwin and Alfred Russell Wallace

In the mid-nineteenth century, the mechanism for evolution was independently conceived of and described by two naturalists: Charles Darwin and Alfred Russel Wallace. Importantly, each naturalist spent time exploring the natural world on expeditions to the tropics. From 1831 to 1836, Darwin traveled around the world to places like South America, Australia, and the southern tip of Africa. Wallace traveled to Brazil to collect insects in the Amazon rainforest from 1848 to 1852 and to the Malay Archipelago from 1854 to 1862. Darwin's journey, as with Wallace's later journeys to the Malay Archipelago, included stops at several island chains, the last being the Galápagos Islands west of Ecuador.

On these islands, Darwin observed that species of organisms on different islands were clearly similar, yet had distinct differences. For example, the ground finches inhabiting the Galápagos Islands comprised several species with unique beak shapes. The species on the islands had a graded series of beak sizes and shapes with very small differences between the most similar. He observed that these finches closely resembled another finch species on the mainland of South America.

Darwin imagined that the island species might be modified from one of the original mainland species. Upon further study, he realized that the varied beaks of each finch helped the birds acquire a specific type of food. For example, seed-eating finches had stronger, thicker beaks for breaking seeds, while insect-eating finches had spear-like beaks for stabbing their prey. In 1860, he wrote, "seeing this gradation and diversity of structure in one small, intimately related group of birds, one might really fancy that from an original paucity of birds in this archipelago, one species had been taken and modified for different ends."

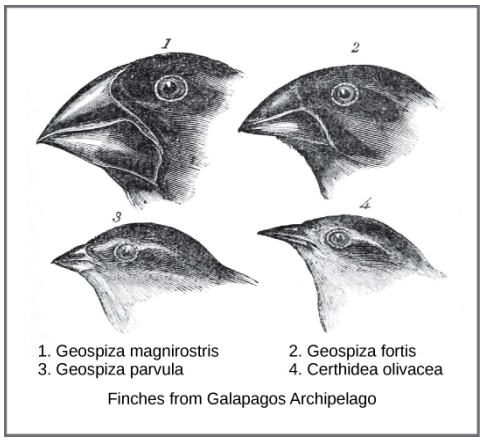


Figure 3.1.2: Darwin observed that beak shape varies among finch species. He postulated that the beak of an ancestral species had adapted over time to equip the finches to acquire different food sources.

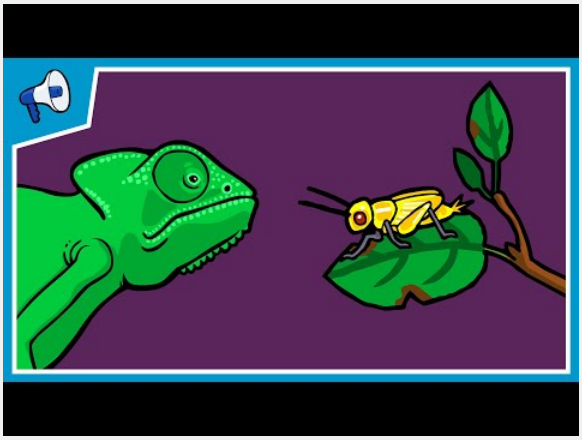
Origin of the Idea of Natural Selection

Wallace and Darwin observed similar patterns in other organisms and independently developed the same explanation for how and why such changes could take place. Darwin called this mechanism natural selection. **Natural selection**, also known as "survival of the fittest," is the more prolific reproduction of individuals with favorable traits that survive environmental change because of those traits. This leads to evolutionary change, the trait becoming predominant within a population. For example, Darwin observed that a population of giant tortoises found in the Galápagos Archipelago have longer necks than those that lived on other islands with dry lowlands. These tortoises were "selected" because they could reach more leaves and access more food than those with short necks. In times of drought, when fewer leaves would be available, those that could reach more leaves had a better chance to eat and survive than those that could not reach the food source. Consequently, long-necked tortoises would more successfully reproduce and pass the long-necked trait to their offspring. Over time, only long-necked tortoises would be present in the population.

Natural selection, Darwin argued, was an inevitable outcome of three principles that operated in nature. First, *most characteristics of organisms are inherited*, or passed from parent to offspring, although *how* traits were inherited was unknown at the time. Second, *more offspring are produced than are able to survive*. The capacity for reproduction in all organisms outstrips the availability of resources to support their numbers. Thus, there is competition for those resources in each generation (note: when Darwin mentioned "survival of the fittest," he was referring to competition between members of the same species for resources, not between different species, a common misconception). Both Darwin and Wallace were influenced by an essay written by economist Thomas Malthus who discussed this principle in relation to human populations. Third, Darwin and Wallace reasoned that *offspring with the inherited characteristics that allow them to best compete for limited resources will survive and have more offspring than those individuals with variations that are less able to compete*. Because characteristics are inherited, these traits will be better represented in the next generation. This will lead to change in populations over successive generations in a process that Darwin called descent with modification. Ultimately, natural selection leads to greater adaptation of the population to its local environment; it is the only mechanism known for adaptive evolution.

Video

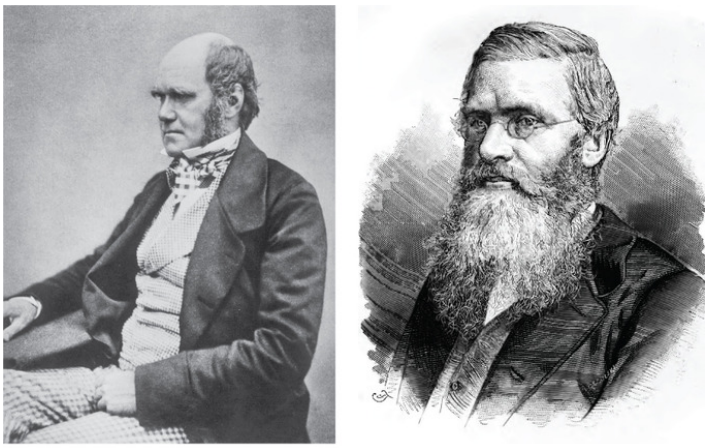




This 9-minute video is an overview of Darwin's concept of natural selection which is explained in a slightly different manner than the reading. Notably, it explains how evolution by natural selection has been harnessed in agriculture and farming.

Question after watching:
Which aspects of natural selection are random and which are not random?

Papers by Darwin and Wallace presenting the idea of natural selection were read together in 1858 before the Linnean Society in London. The following year, Darwin's book, *On the Origin of Species*, was published which outlined his arguments for evolution by natural selection.



(a) (b)

Figure 3.1.3: Both (a) Charles Darwin and (b) Alfred Wallace wrote scientific papers on natural selection that were presented together before the Linnean Society in 1858.

? Optional Activity 3.1.1

Which scientific concept did Charles Darwin and Alfred Russell Wallace independently discover?

a. mutation
b. natural selection
c. overbreeding
d. sexual reproduction

Answer

b. natural selection

Requirements for Evolution

All of the following are required for evolution to occur.

Variation

One of the hallmarks of Darwin and Wallace's theory of evolution via natural selection is that it can only take place if there is **variation**, or differences, among individuals in a population. Importantly, these differences must have a genetic basis (their **genotypes**); otherwise, selection will not lead to change in the next generation. This is critical because variation among individuals can be caused by non-genetic reasons, such as an individual losing a limb due to an accident. Variations of this type would not be inherited by the next generation.

Individuals of a population often display different **phenotypes**, or physical, metabolic, or behavioral expressions of their genotypes. Populations with two or more variations of particular characteristics, or trait, are called **polymorphic**. The distribution of phenotypes among individuals, known as the **population variation**, is influenced by a number of factors, including the population's genetic structure and the environment (Figure 3.1.4). Understanding the sources of a phenotypic variation in a population is important for determining how a population will evolve in response to different evolutionary pressures.



Figure 3.1.4: The distribution of phenotypes in this litter of kittens illustrates population variation. (credit: Pieter Lanser)

The theory of natural selection stems from the observation that some individuals in a population are more likely to survive longer and have more offspring than others; thus, they will pass on more of their genes to the next generation. A big, powerful male gorilla, for example, is much more likely than a smaller, weaker one to become the population's silverback, the pack's leader who mates far more than the other males of the group. The pack leader will father more offspring, who share half of his genes, and are likely to also grow bigger and stronger like their father. Over time, the genes for bigger size will increase in frequency in the population, and the population will, as a result, grow larger on average. That is, this would occur if this particular **selection pressure**, or driving selective force, were the only one acting on the population. In other examples, better camouflage or a stronger resistance to drought might pose a selection pressure. In addition to natural selection, below are the details of five other agents of evolutionary change that are all acting in concert with natural selection.

This variation, or **genetic diversity,** within a population comes from two main mechanisms: mutation and sexual reproduction. **Mutation**, a change in the DNA sequence, is the ultimate source of new alleles, or new genetic variation in any population. The genetic changes caused by mutation can have one of three outcomes:

- Many mutations will have no effect on the genetic contribution of an individual to future generations; these are called neutral mutations.
- A mutation may affect the phenotype of the organism in a way that gives it a lower likelihood of survival or fewer offspring.
- A mutation may produce a phenotype with a beneficial effect on survival or its genetic contribution to future generations.

Different mutations will have a range of above effects on an organism that expresses them in their phenotype, from a small to great.

Sexual reproduction also leads to genetic diversity: when two individuals of a sexually-reproducing species reproduce, unique combinations of alleles assemble to produce the unique genotypes and thus phenotypes in each of the offspring. However, sexual reproduction does not lead to *new* genes, but rather provides a new combination of genes in a given individual.

Inheritance

The trait or adaptation being selected for or against must be heritable.

Differential Reproduction and Survival

Individuals with a certain version of the trait are more likely to survive and reproduce than individuals with a different version of the trait

Time

The version of the trait that helps individuals survive and reproduce becomes more common in the population over multiple generations. Individuals do not evolve.

? Optional Activity 3.1.2

Which of the following situations may lead to natural selection?

a. The seeds of two plants land near each other and one grows larger faster.
b. Two types of fish eat the same kind of food but one is better able to gather food than the other.
c. In a species of fungi, one colony spreads faster through the soil to reach nutrients than another colony of the same species.
d. All of the above may lead to natural selection.

Answer

d. All of the above may lead to natural selection.

Patterns of Evolution

The evolution of species has resulted in enormous variation in form and function. Sometimes, evolution gives rise to groups of organisms that become tremendously different from each other. We call two species that evolve in diverse directions from a common point **divergent evolution**. We can see such divergent evolution in the forms of the reproductive organs of flowering plants which share the same basic anatomies (Figure 3.1.5); however, they can look very different as a result of selection in different physical environments and adaptation to different kinds of pollinators.



Figure 3.1.5: Flowering plants evolved from a common ancestor. Notice that the (a) dense blazing star (Liatrus spicata) and the (b) purple coneflower (Echinacea purpurea) vary in appearance, yet both share a similar basic morphology.

In other cases, similar phenotypes evolve independently in distantly related species. For example, flight has evolved in both bats and insects, and they both have structures we refer to as wings, which are adaptations to flight. However, bat and insect wings have evolved from very different original structures. We call this phenomenon **convergent evolution**, where similar traits evolve independently in species that do not share a common ancestry. The two species came to the same function, flying, but did so separately from each other.

These physical changes occur over enormous time spans and help explain how evolution occurs. Natural selection acts on individual organisms, which can then shape an entire species. Although natural selection may work in a single generation on an individual, it can take thousands or even millions of years for an entire species' genotype to evolve. It is over these large time spans that life on earth has changed and continues to change.

? Optional Activity 3.1.3

Which situation is most likely an example of convergent evolution?

a. Squid and humans have eyes similar in structure.
b. Worms and snakes both move without legs.
c. Some bats and birds have wings that allow them to fly.
d. All of the above are examples of convergent evolution.

Answer

D. All of the above are examples of convergent evolution.

The Modern Synthesis: Natural Selection and Genetics

The mechanisms of inheritance, **genetics**, were not understood at the time Darwin and Wallace were developing their idea of natural selection. This lack of understanding was a stumbling block to comprehending many aspects of evolution. In fact, blending inheritance was the incorrect, but predominant, genetic theory of the time. This made it difficult to understand how natural

selection might operate. Darwin and Wallace were unaware of the genetics work by Austrian monk Gregor Mendel, which was published in 1866, not long after the publication of *On the Origin of Species*. Mendel's work was rediscovered in the early twentieth century at which time geneticists were rapidly coming to an understanding of the basics of inheritance. Initially, the newly discovered particulate nature of genes made it difficult for biologists to understand how gradual evolution could occur. But over the next few decades, genetics and evolution were integrated into what became known as the **modern synthesis**—the coherent understanding of the relationship between natural selection and genetics that took shape by the 1940s and is generally accepted today. In sum, the modern synthesis describes how evolutionary pressures, such as natural selection, can affect a population's genetic makeup, and, in turn, how this can result in the gradual evolution of populations and species. The theory also connects this gradual change of a population over time, called **microevolution**, with the processes that gave rise to new species and higher taxonomic groups with widely divergent characters, called **macroevolution**.

Misconceptions about Evolution

The theory of evolution has been amply tested by researchers over the past 200 years. From this work, confidence in the theory's basic tenants has been bolstered. Today, the vast majority of scientists accept the theory of evolution by natural selection as the most plausible, supported mechanism to explain how organisms change over time.

However, certain groups, led by values other than scientific search for evidence, have objected to the theory of evolution including as an explanation for the diversity of life. This has led to the spread of some misinformation and misconception about the theory. Below, these misconceptions are explicitly addressed.

Concept in Action

This website addresses some of the main misconceptions associated with the theory of evolution.

Misconception #1: Evolution Is Just a 'Theory'

Critics of the theory of evolution dismiss its importance by purposefully confounding the everyday usage of the word "theory" with the way scientists use the word. In science, a **theory** is understood to be a concept that has been extensively tested and supported over time. We have a theory of the atom, a theory of gravity, and the theory of relativity, each of which describes the strong evidence that scientists have to support our understanding of nature and the universe. In the same way, the theory of evolution describes our scientific understanding about life. As such, a theory in science has survived significant efforts to discredit it by scientists, who are naturally skeptical. While theories can sometimes be overturned or revised, this does not lessen their weight but simply reflects the constantly evolving state of scientific knowledge. In contrast, a "theory" in common vernacular means a guess or suggested explanation for something. This meaning is more along the lines of the concept of a scientific **hypothesis**, which is a tentative explanation for something that is proposed to either be supported or disproved. When critics of evolution say evolution is "just a theory," they are mischaracterizing the science and inferring that there is little evidence supporting it. This is far from accurate. Evolution is widely accepted, extensively tested, heavily supported, and can be monitored in real-time, such as with Darwin's finches.

Misconception #2: Individuals Evolve

An individual is born with the genes it has—these do not change as the individual ages. Therefore, an individual cannot evolve or adapt through natural selection. Individuals do change over their lifetime, but this is called development; it involves changes programmed by the set of genes the individual acquired at birth in coordination with the individual's environment. When thinking about the evolution of a characteristic, it is probably best to think about the change in the average value of the characteristic in the population over time. For example, when natural selection leads to bill-size change in medium ground finches in the Galápagos, this does not mean that individual bills on the finches are changing. If one measures the average bill size among all individuals in the population at one time, and then measures the average bill size in the population several years later after there has been a strong selective pressure, this average value may be different as a result of evolution. Although some individuals may survive from the first time to the second, those individuals will still have the same bill size. However, there may be enough new individuals with different bill sizes to change the average bill size.

Misconception #3: Evolution Explains the Origin of Life

It is a common misunderstanding that evolution includes an explanation of life's origins. Conversely, some of the theory's critics complain that it cannot explain the origin of life. The theory of evolution explains how populations change over time and how life diversifies—the origin of species. It does not shed light on the beginnings of life including the origins of the first cells, which is how life is defined. The mechanisms of the origin of life on Earth are a particularly difficult problem because it occurred a very long time ago, over a very long time, and presumably just occurred once. Importantly, biologists believe that the presence of life on Earth precludes the possibility that the events that led to life on Earth can be repeated because the intermediate stages would immediately become food for existing living things. The early stages of life included the use or formation of organic molecules such as carbohydrates, amino acids, or nucleotides. If these were formed from inorganic precursors today, they would simply be broken down by living things. The early stages of life also probably included more complex aggregations of molecules into enclosed structures with an internal environment, a boundary layer of some form, and an external environment. Such structures, if they were formed now, would be quickly consumed or broken down by living organisms.

However, once a mechanism of inheritance was in place in the form of a molecule like DNA or RNA, either within a cell or within a pre-cell, these entities would be subject to the principle of natural selection. More effective reproducers would increase in frequency at the expense of inefficient reproducers. So while evolution does not explain the origin of life, it may have something to say about some of the processes operating once pre-living entities acquired certain properties.

Misconception #4: Organisms Evolve on Purpose

Statements such as "organisms evolve in response to a change in an environment," are quite common. There are two easy misunderstandings possible with such a statement. First of all, the statement must not be understood to mean that individual organisms evolve, as was discussed above. The statement is shorthand for "a population evolves in response to a changing environment." However, a second misunderstanding may arise by interpreting the statement to mean that the evolution is somehow intentional. A changed environment results in some individuals in the population, those with particular phenotypes, benefiting and, therefore, producing proportionately more offspring than other phenotypes. This results in a change in the population if the characters are genetically determined.

It is also important to understand that the variation that natural selection works on is already in a population and does not arise in response to an environmental change. For example, applying antibiotics to a population of bacteria will, over time, select for a population of bacteria that are resistant to antibiotics. The resistance, which is caused by a gene, did not arise by mutation because of the application of the antibiotic. The gene for resistance was already present in the gene pool of the bacteria, likely at a low frequency. The antibiotic, which kills the bacterial cells without the resistance gene, strongly selects for individuals that are resistant, since these would be the only ones that survived and divided. Experiments have demonstrated that mutations for antibiotic resistance do not arise as a result of the antibiotic application.

In a larger sense, evolution is also not goal-directed. Species do not become "better" over time; they simply track their changing environment with adaptations that maximize their reproduction in a particular environment at a particular time. Evolution has no goal of making faster, bigger, more complex, or even smarter species. This kind of language is common in popular literature. Certain organisms, ourselves included, are described as the "pinnacle" of evolution, or "perfected" by evolution. What characteristics evolve in a species are a function of the variation present and the environment, both of which are constantly changing in a non-directional way. What trait is fit in one environment at one time may well be fatal at some point in the future. This holds equally well for a species of insect as it does for the human species.

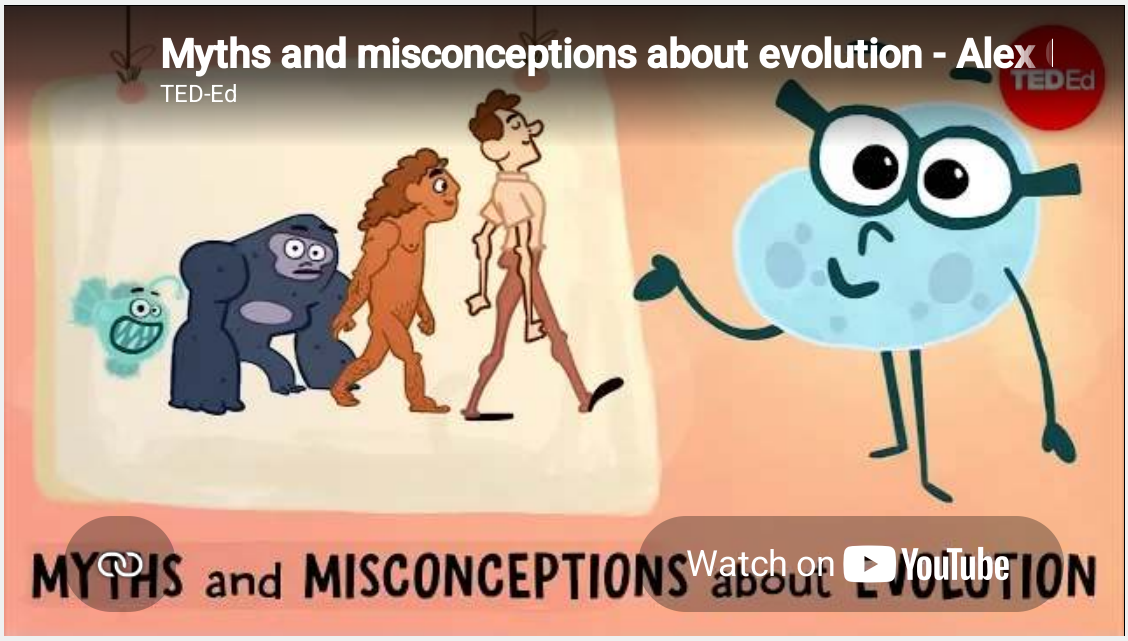
Misconception #5: Evolution Is Controversial among Scientists

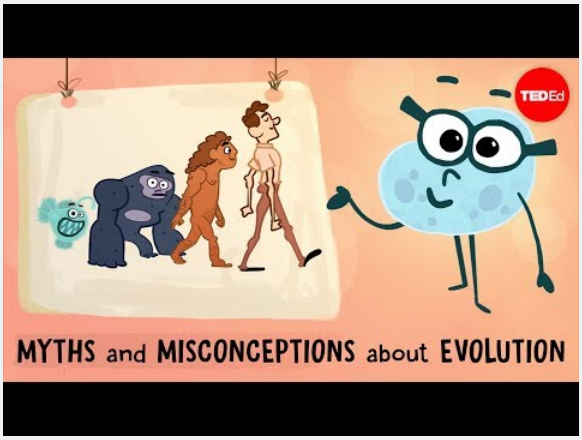
The theory of evolution was controversial when it was first proposed in 1859, yet within 20 years virtually every working biologist had accepted evolution as the explanation for the diversity of life. The rate of acceptance was extraordinarily rapid, partly because Darwin had amassed an impressive body of evidence. The early controversies involved both scientific arguments against the theory and the arguments of religious leaders. It was the arguments of the biologists that were resolved after a short time, while the arguments of religious leaders have persisted to this day.

The number of working scientists who reject the theory of evolution, or question its validity and say so, is small. A Pew Research poll in 2009 found that 97 percent of the 2500 scientists polled believe species evolve.[2] The support for the theory is reflected in

signed statements from many scientific societies such as the American Association for the Advancement of Science, which includes working scientists as members. Many of the scientists who reject or question the theory of evolution are non-biologists, such as engineers, physicians, and chemists. There are no experimental results or research programs that contradict the theory. There are no papers published in peer-reviewed scientific journals that appear to refute the theory. The latter observation might be considered a consequence of the suppression of dissent, but it must be remembered that scientists are skeptics and that there is a long history of published reports that challenged scientific orthodoxy in unpopular ways. Examples include the endosymbiotic theory of eukaryotic origins, the theory of group selection, the microbial cause of stomach ulcers, the asteroid-impact theory of the Cretaceous extinction, and the theory of plate tectonics. Research with evidence and ideas with scientific merit are considered by the scientific community. Research that does not meet these standards is rejected.

Video





This 4-minute video provides an overview of the main misconceptions about evolution, how they came to be, and what the accurate interpretation should be.

Question after watching:

How can the expression "survival of the fittest" be misunderstood? Explain how it can be misunderstood and the accurate concept.

Footnotes

1. 1 Theodosius Dobzhansky. “Biology, Molecular and Organismic.” *American Zoologist* 4, no. 4 (1964): 449.
2. 2 Pew Research Center for the People & the Press, *Public Praises Science; Scientists Fault Public, Media* (Washington, DC, 2009), 37.Contributors

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3.2: Evidence of Evolution

Evidence of Evolution

- Please read and watch the following Mandatory Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 2.5 hours.
- To navigate to the next Section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Explain how a variety of forms of evidence support the theory of evolution.

Evolution - It's a Thing

Video



This 11-minute video describes the formation of fossils.
Question after watching: What were the forms of evidence highlighted that inform scientists about whale evolution?

Modern Studies of Darwin's Finches - Evidence of Natural Selection

Scientific studies of evolution by natural selection can be time-consuming. One of the best demonstrations has been in the very birds that helped to inspire the theory, the Galápagos finches. Peter and Rosemary Grant and their colleagues have studied Galápagos finch populations every year since 1976 and have provided important demonstrations of the operation of natural selection. The Grants found changes from one generation to the next in the beak shapes of the medium ground finches on the Galápagos island of Daphne Major. The medium ground finch feeds on seeds. The birds have inherited variations in the bill shape with some individuals having wide, deep bills and others having thinner bills. Large-billed birds feed more efficiently on large, hard seeds, whereas smaller billed birds feed more efficiently on small, soft seeds.

During 1977, a drought period altered vegetation on the island. After this period, the number of seeds declined dramatically: the decline in small, soft seeds was greater than the decline in large, hard seeds. The large-billed birds were able to survive better than the small-billed birds the following year. The year following the drought when the Grants measured beak sizes in the much-reduced population, they found that the average bill size was larger (Figure 3.2.3). This was clear evidence for natural selection (differences in survival) of bill size caused by the availability of seeds.

The Grants had studied the inheritance of bill sizes and knew that the surviving large-billed birds would tend to produce offspring with larger bills, so the selection would lead to evolution of bill size. Subsequent studies by the Grants have demonstrated selection

on and evolution of bill size in this species in response to changing conditions on the island. The evolution has occurred both to larger bills, as in this case, and to smaller bills when large seeds became rare.

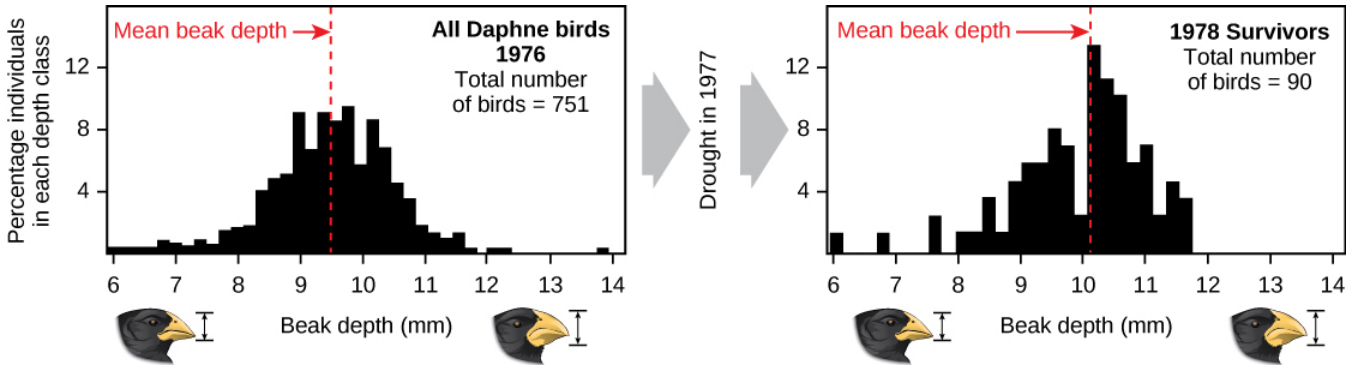


Figure 3.2.1: A drought on the Galápagos island of Daphne Major in 1977 reduced the number of small seeds available to finches, causing many of the small-beaked finches to die. This caused an increase in the finches' average beak size between 1976 and 1978.

The Fossil Record as Evidence for Evolution

Fossils tell us when organisms lived, as well as provide evidence for the progression and evolution of life on earth over millions of years.

Fossils are the preserved remains or traces of animals, plants, and other organisms from the past. Fossils range in age from 10,000 to 3.48 billion years old. The observation that certain fossils were associated with certain rock strata led 19th-century geologists to recognize a geological timescale. Like extant organisms, fossils vary in size from microscopic, like single-celled bacteria, to gigantic, like dinosaurs and trees.



Figure 3.2.2: "Sue": The bones of this *Tyrannosaurus rex* were preserved through the process of permineralization, which suggests that this organism was covered by sediment soon after death.

Permineralization

Permineralization is a process of fossilization that occurs when an organism is buried. Small-scale permineralization can produce very detailed fossils. For permineralization to occur, the organism must be covered by sediment soon after death, or soon after the initial decay process.

It would not be an exaggeration to say that the typical vertebrate fossil consists of a single bone, or tooth, or fish scale. The preservation of an intact skeleton with the bones in the relative positions they had in life requires remarkable circumstances. The mineralization of soft parts is even less common and is seen only in exceptionally rare chemical and biological conditions.

Some of the best fossil beds in the world are located in Canada, due to the vast age of the rocks in the shield formations there. Alberta is well known for its *T. rex*, *Albertasaurus*, and *Edmontonsaurus* specimens. Fossils in the Burgess Shale, located between Alberta and British Columbia, date back even further to before the Cabrian Explosion more than 550 million years ago!



a b

Figure 3.2.3: Dinosaur National Park in Alberta. (a) Scientists must be careful with their footing as small fossils abound.(b) A trilobite fossil. (Copyright; CC-BY-SA 4.0 Annie Prud'homme Genereux)

Video





This 4-minute video humorously describes the formation of fossils.
Question after watching:
If you were a paleontologist, where would you go to look for a fossil?

Trace Fossils

Fossils may also consist of the marks left behind by the organism while it was alive, such as footprints or feces. These types of fossils are called **trace fossils**, or ichnofossils, as opposed to body fossils. Past life may also leave some markers that cannot be seen but can be detected in the form of biochemical signals; these are known as chemofossils or biomarkers.



Figure 3.2.4: These dinosaur footprints, examples of trace fossils, are located in Denver, Colorado's Dino Ridge. Similar footprints can be seen in Grande Prarie in Northern Alberta and Northern British Columbia (CC-BY-SA 4.0 Annie Prud'homme Genereux).

The Fossil Record

The totality of fossils, both discovered and undiscovered, and their placement in fossiliferous (fossil-containing) rock formations and sedimentary layers (strata) is known as the **fossil record**. The fossil record was one of the early sources of data underlying the study of evolution and continues to be relevant to the history of life on Earth. The development of radiometric dating techniques in the early 20th-century allowed geologists to determine the numerical or “absolute” age of various strata and their included fossils.

Each fossil discovery represents a snapshot of the process of evolution. Because of the specialized and rare conditions required for a biological structure to fossilize, many important species or groups may never leave fossils at all. Even if they do leave fossils, humans may never find them—for example, if they are buried under hundreds of feet of ice in Antarctica. The number of species discovered through the fossil record is less than 5% of the number of species alive today. Fossilized species may represent less than 1% of all the species that have ever lived.

The fossil record is very uneven and is mostly comprised of fossils of organisms with hard body parts, leaving most groups of soft-bodied organisms with little to no fossil record. Groups considered to have a good fossil record, including transitional fossils between these groups, are the vertebrates, the echinoderms, the brachiopods, and some groups of arthropods. Their hard bones and shells fossilize easily, unlike the bodies of organisms like cephalopods or jellyfish.

Romer’s gap is an example of an apparent gap in the tetrapod fossil record used in the study of evolutionary biology. These gaps represent periods from which no relevant fossils have been found. Romer’s gap is named after paleontologist Alfred Romer, who first recognized it. Romer’s gap spanned from approximately 360 to 345 million years ago, corresponding to the first 15 million years of the Carboniferous Period. There has been much debate over why there are so few fossils from this time period. Some scientists have suggested that the geochemistry of the time period caused bad conditions for fossil formation, so few organisms were fossilized. Another hypothesis suggests that scientists have simply not yet discovered an excavation site for these fossils, due to inaccessibility or random chance.



Figure 3.2.5: The bank of the Whiteadder Water in Scotland is one of the few known localities bearing fossils of tetrapods from Romer's gap.

Determining Fossil Ages

Paleontology seeks to map out how life evolved across geologic time. A substantial hurdle is in the difficulty of working out fossil ages. There are several different methods for estimating the ages of fossils, including:

1. stratigraphy
2. biostratigraphy
3. carbon dating

Stratigraphy

Paleontologists rely on stratigraphy to date fossils. **Stratigraphy** is the science of understanding the strata, or layers, that form the sedimentary record. Strata are differentiated from each other by their different colors or compositions and are exposed in cliffs, quarries, and river banks. These rocks normally form relatively horizontal, parallel layers, with younger layers forming on top.

If a fossil is found between two layers of rock whose ages are known, the fossil's age is thought to be between those two known ages. Because rock sequences are not continuous but may be broken up by faults or periods of erosion, it is difficult to match up rock beds that are not directly adjacent.



Figure 3.2.6: The layers of sedimentary rock, or strata, can be seen as horizontal bands of differently colored or differently structured materials exposed in this cliff. The deeper layers are older than the layers found at the top, which aids in determining the relative age of fossils found within the strata.

Biostratigraphy

Fossils of species that survived for a relatively short time can be used to match isolated rocks: this technique is called **biostratigraphy**. For instance, the extinct chordate *Eoplacognathus pseudoplanus* is thought to have existed during a short time in the Middle Ordovician period. If rocks of unknown age have traces of *E. pseudoplanus*, they have a mid-Ordovician age. Such index fossils must be distinctive, globally distributed, and occupy a short time range to be useful. Misleading results can occur if the index fossils are incorrectly dated.

Relative Dating

Stratigraphy and biostratigraphy can in general provide only relative dating (A was before B), which is often sufficient for studying evolution. This is difficult for some time periods, however, because of the barriers involved in matching rocks of the same age across continents. Family-tree relationships can help to narrow down the date when lineages first appeared. For example, if fossils of B date to X million years ago and the calculated "family tree" says A was an ancestor of B, then A must have evolved earlier.

It is also possible to estimate how long ago two living branches of a family tree diverged by assuming that DNA mutations accumulate at a constant rate. However, these "**molecular clocks**" are sometimes inaccurate and provide only approximate timing. For example, they are not sufficiently precise and reliable for estimating when the groups that feature in the Cambrian explosion first evolved, and estimates produced by different approaches to this method may vary as well.

Carbon Dating

Together with stratigraphic principles, radioactive elements are used in geochronology to establish the geological time scale. Beds that preserve fossils typically lack these traditional radioactive elements. Instead, **radiocarbon dating**, or simply "carbon dating", is used Figure 3.2.7. The principle of radiocarbon dating is simple: the rates at which various radioactive elements decay are known, and the ratio of the radioactive element to its decay products shows how long the radioactive element has existed in the rock. This rate is represented by the half-life, which is the time it takes for half of a sample to decay.

The half-life of carbon-14 is 5,730 years, so carbon dating is only relevant for dating fossils less than 60,000 years old. Radioactive elements are common only in rocks with a volcanic origin, so the only fossil-bearing rocks that can be dated using traditional elements are volcanic ash layers. Carbon dating uses the decay of carbon-14 to estimate the age of organic materials, such as wood and leather.

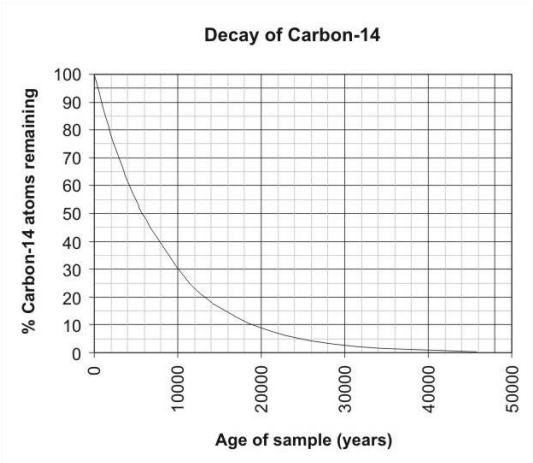


Figure 3.2.7: Radiocarbon dating is a technique used to date carbon in rocks or fossils usually based on a comparison between the observed abundance of a naturally occurring radioactive isotope (in this case, carbon-14) and its decay products, using known decay rates.

Case Study: The Fossil Record and the Evolution of the Modern Horse

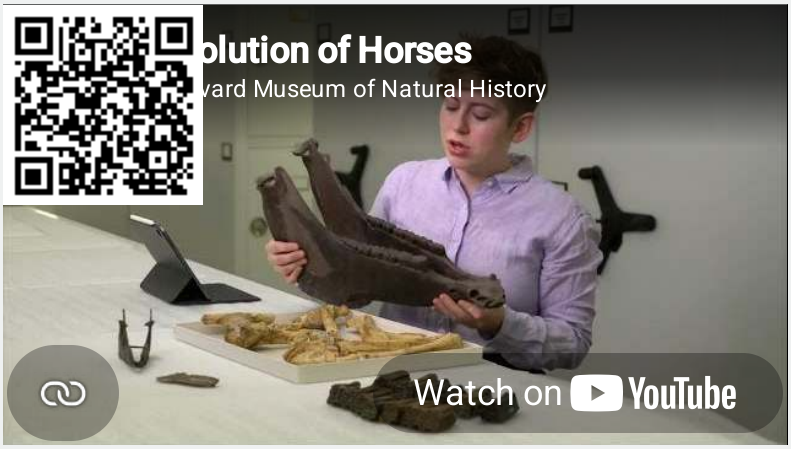
Highly detailed fossil records have been recovered for sequences in the evolution of modern horses. The fossil record of horses in North America is especially rich and contains transition fossils: fossils that show intermediate stages between earlier and later forms. The fossil record extends back to a dog-like ancestor some 55 million years ago, which gave rise to the first horse-like species 55 to 42 million years ago in the genus *Eohippus*.

The first *Equid* fossil was found in the gypsum quarries in Montmartre, Paris in the 1820s. The tooth was sent to the Paris Conservatory, where Georges Cuvier identified it as browsing equine, related to the tapir. His sketch of the entire animal matched later skeletons found at the site. During the H.M.S. Beagle survey expedition, Charles Darwin had remarkable success with fossil hunting in Patagonia. In 1833 in Santa Fe, Argentina, he was "filled with astonishment" when he found a horse's tooth in the same stratum as fossils of giant armadillos and wondered if it might have been washed down from a later layer, but concluded this was

"not very probable." In 1836, the anatomist Richard Owen confirmed the tooth was from an extinct species, which he subsequently named *Equus curvidens*.

The original sequence of species believed to have evolved into the horse was based on fossils discovered in North America in the 1870s by paleontologist Othniel Charles Marsh. The sequence, from *Eohippus* to the modern horse (*Equus*), was popularized by Thomas Huxley and became one of the most widely known examples of a clear evolutionary progression. The sequence of transitional fossils was assembled by the American Museum of Natural History into an exhibit that emphasized the gradual, "straight-line" evolution of the horse.

Video



This video explains how fossils show dramatic changes in horse morphology over nearly 60 million years of evolution.

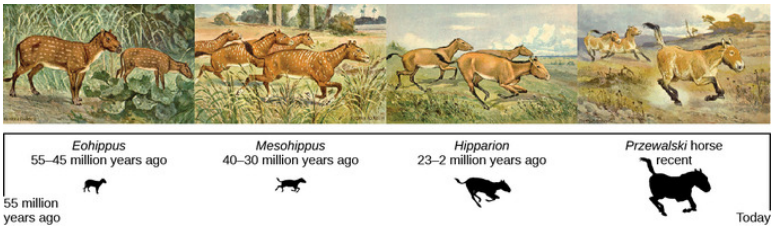


Figure 3.2.8: This illustration shows an artist's renderings of species derived from fossils of the evolutionary history of the horse and its ancestors. The species depicted are only four from a very diverse lineage that contains many branches, dead ends, and adaptive radiations. One of the trends, depicted here, is the evolutionary tracking of a drying climate and increase in prairie versus forest habitat reflected in forms that are more adapted to grazing and predator escape through running.

Since then, as the number of *Equid* fossils has increased, the actual evolutionary progression from *Eohippus* to *Equus* has been discovered to be much more complex and multi-branched than was initially supposed. Detailed fossil information on the rate and distribution of new *Equid* species has also revealed that the progression between species was not as smooth and consistent as was once believed.

Although some transitions were indeed gradual progressions, a number of others were relatively abrupt in geologic time, taking place over only a few million years. Both **anagenesis**, a gradual change in an entire population's gene frequency, and **cladogenesis**, a population "splitting" into two distinct evolutionary branches, occurred, and many species coexisted with "ancestor" species at various times.

Adaptation for Grazing

The series of fossils tracks the change in anatomy resulting from a gradual drying trend that changed the landscape from a forested habitat to a prairie habitat. Early horse ancestors were originally specialized for tropical forests, while modern horses are now adapted to life on drier land. Successive fossils show the evolution of teeth shapes and foot and leg anatomy to a grazing habit with adaptations for escaping predators.

The horse belongs to the order Perissodactyla (odd-toed ungulates), the members of which all share hoofed feet and an odd number of toes on each foot, as well as mobile upper lips and a similar tooth structure. This means that horses share a common ancestry with tapirs and rhinoceroses. Later species showed gains in size, such as those of *Hipparion*, which existed from about 23 to 2 million years ago. The fossil record shows several adaptive radiations in the horse lineage, which is now much reduced to only one genus, *Equus*, with several species. Paleozoologists have been able to piece together a more complete outline of the modern horse's evolutionary lineage than that of any other animal.

Additional Evidence for Evolution

Homologous Structures vs Analagous Structures

Homology is the relationship between structures or DNA derived from the most recent common ancestor. A common example of **homologous structures** in evolutionary biology is the wings of bats and the arms of primates. Although these two structures do not look similar or have the same function, genetically, they come from the same structure from the last common ancestor. Homologous traits of organisms are therefore explained by descent from a common ancestor. In genetics, homology is measured by comparing protein or DNA sequences. Homologous gene sequences share a high similarity, supporting the hypothesis that they share a common ancestor. It's important to note that defining two structures or sequences as homologous depends on what ancestor is being described as the common ancestor.

Homology can also be partial: new structures can evolve through the combination of developmental pathways or parts of them. As a result, hybrid or mosaic structures can evolve that exhibit partial homologies. For example, certain compound leaves of flowering plants are partially homologous both to leaves and shoots because they combine some traits of leaves and some of shoots.

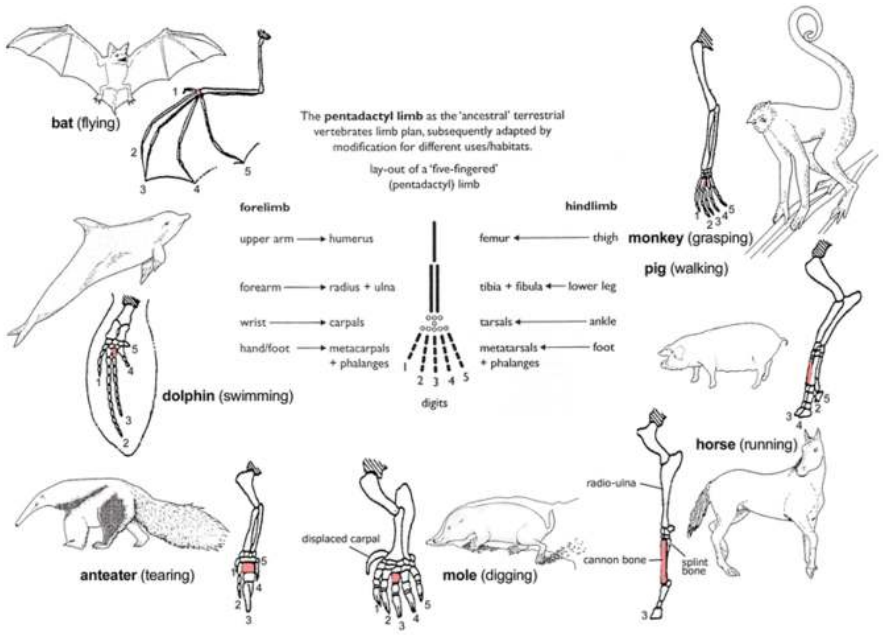


Figure 3.2.9: The principle of homology illustrated by the adaptive radiation of the forelimb of mammals. All conform to the basic pentadactyl pattern but are modified for different usages. The third metacarpal is shaded throughout; the shoulder is crossed-hatched.

The opposite of homologous structures is **analogous structures**, which are physically similar structures between two taxa that evolved separately (rather than being present in the last common ancestor). Bat wings and bird wings evolved independently and are considered analogous structures. Genetically, a bat wing and a bird wing have very little in common; the last common ancestor of bats and birds did not have wings like either bats or birds. Wings evolved independently in each lineage after diverging from ancestors with forelimbs that were not used as wings (terrestrial mammals and theropod dinosaurs, respectively).

It is important to distinguish between different hierarchical levels of homology in order to make informative biological comparisons. In the above example, the bird and bat wings are analogous as wings, but homologous as forelimbs because the organ

served as a forearm (not a wing) in the last common ancestor of tetrapods.

Analogy is different than homology. Although analogous characteristics are superficially similar, they are not homologous because they are phylogenetically independent. The wings of a maple seed and the wings of an albatross are analogous but not homologous (they both allow the organism to travel on the wind, but they did not both develop from the same structure).

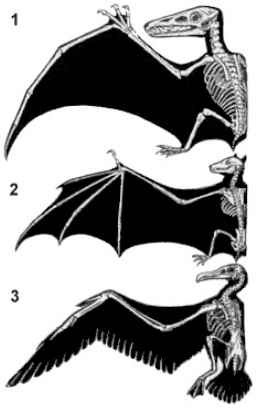


Figure 3.2.10: The wings of pterosaurs (1), bats (2), and birds (3) are analogous as wings, but homologous as forelimbs. This is because they are similar characteristically and even functionally, but evolved from different ancestral roots.

Vestigial Structures

Some organisms possess structures with no apparent function which appear to be residual parts from a past ancestor. For example, some snakes have pelvic bones despite having no legs because they descended from reptiles that did have legs. Another example of a structure with no function is the human vermiform appendix. These unused structures without function are called **vestigial structures**. Other examples of vestigial structures are wings (which may have other functions) on flightless birds like the ostrich, leaves on some cacti, traces of pelvic bones in whales, and the sightless eyes of cave animals.

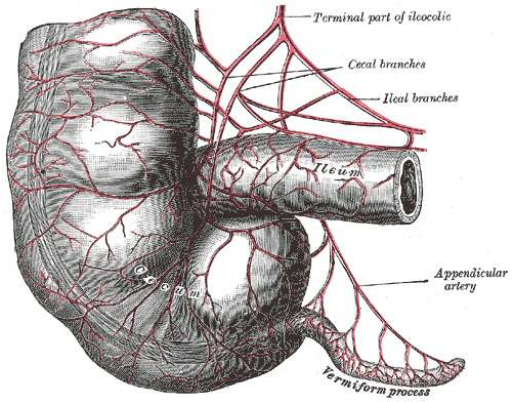


Figure 3.2.11: In humans, the appendix is a vestigial structure; it has lost much of its ancestral function.

There are also several reflexes and behaviors that are considered to be vestigial. The formation of goosebumps in humans under stress is a vestigial reflex its function in human ancestors was to raise the body's hair, making the ancestor appear larger and scaring off predators. The arrector pili muscle, which is a band of smooth muscle that connects the hair follicle to connective tissue, contracts and creates goosebumps on the skin.

Vestigial Structures in Evolution

Vestigial structures are often homologous to structures that function normally in other species. Therefore, vestigial structures can be considered evidence for evolution, the process by which beneficial heritable traits arise in populations over an extended period of time. The existence of vestigial traits can be attributed to changes in the environment and behavior patterns of the organism in question. As the function of the trait is no longer beneficial for survival, the likelihood that future offspring will inherit the "normal" form of it decreases. If there are no selection pressures actively lowering the fitness of the individual, the trait will persist in future generations unless the trait is eliminated through genetic drift or other random events.

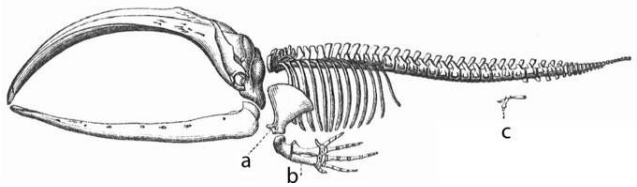
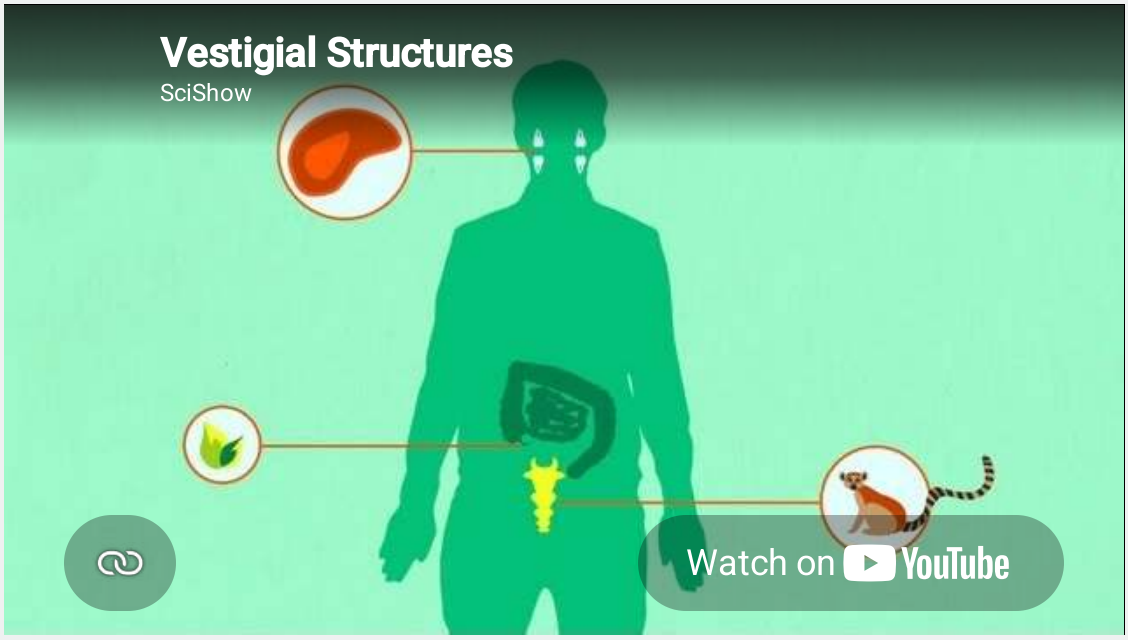


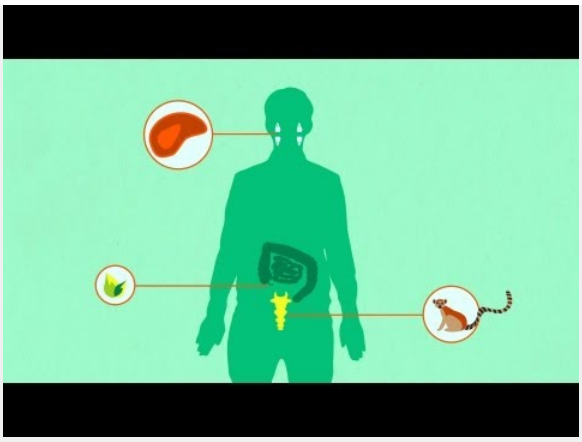
Figure 3.2.12: The pelvic bones in whales are also a good example of vestigial evolution (whales evolved from four-legged land mammals and secondarily lost their hind legs). Letter c in the picture indicates the undeveloped hind legs of a baleen whale.

In some cases, the structure becomes detrimental to the organism. Although in many cases the vestigial structure is of no direct harm, all structures require extra energy in terms of development, maintenance, and weight and are also a risk in terms of disease (e.g., infection, cancer). This provides some selective pressure for the removal of parts that do not contribute to an organism's fitness, but a structure that is not directly harmful will take longer to be 'phased out' than one that is. Some vestigial structures persist due to limitations in development, such that complete loss of the structure could not occur without major alterations of the organism's developmental pattern, and such alterations would likely produce numerous negative side effects.

The vestigial versions of a structure can be compared to the original version of the structure in other species in order to determine the homology of the structure. Homologous structures indicate common ancestry with those organisms that have a functional version of the structure. Vestigial traits can still be considered adaptations because an adaptation is often defined as a trait that has been favored by natural selection. Adaptations, therefore, need not be adaptive, as long as they were at some point.

Video





This 4-minute video takes you on a tour of vestigial structures in the human body.
Question after watching: We say that vestigial structures are evidence for evolution. Why is that? What could account for these structures if evolution was not the reason?

Convergent Evolution

Sometimes, similar phenotypes evolve independently in distantly related species. For example, flight has evolved in both bats and insects, and they both have wings, which are adaptations to flight. However, the wings of bats and insects have evolved from very different original structures. This phenomenon is called **convergent evolution**, where similar traits evolve independently in species that do not share a recent common ancestry.

Examples of Convergent Evolution

Convergent evolution describes the independent evolution of similar features in species of different lineages. The two species came to the same function, flying, but did so separately from each other. They have "converged" on this useful trait. Both sharks and dolphins have similar body forms, yet are only distantly related: sharks are fish and dolphins are mammals. Such similarities are a result of both populations being exposed to the same selective pressures. Within both groups, changes that aid swimming have been favored. Thus, over time, they developed similar appearances (morphology), even though they are not closely related.

One of the most well-known examples of convergent evolution is the camera eye of cephalopods (e.g., octopus), vertebrates (e.g., mammals), and cnidaria (e.g., box jellies). Their last common ancestor had at most a very simple photoreceptive spot, but a range of processes led to the progressive refinement of this structure to the advanced camera eye. There is, however, one subtle difference: the cephalopod eye is "wired" in the opposite direction, with blood and nerve vessels entering from the back of the retina, rather than the front as in vertebrates.

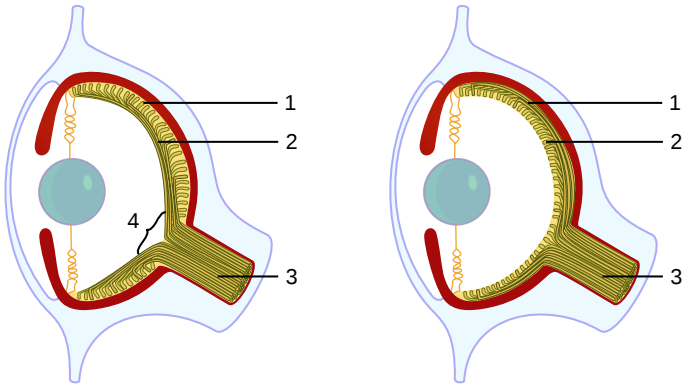


Figure 3.2.13: Vertebrates and octopuses developed the camera eye independently. In the vertebrate version (left), the nerve fibers pass in front of the retina, and there is a blind spot (4) where the nerves pass through the retina. In the octopus version (right), the eye is constructed the "right way out," with the nerves attached to the rear of the retina. This means that octopuses do not have a blind spot.

The opposite of convergent evolution is **divergent evolution**, whereby related species evolve different traits. On a molecular level, this can happen due to random mutation unrelated to adaptive changes. More will be discussed on divergent evolution in Unit 2.3.

Biogeography and the Modern Distribution of Species

Biogeography is the study of the geographic distribution of living things and the abiotic factors that affect their distribution. Abiotic factors, such as temperature and rainfall, vary based on latitude and elevation, primarily. As these abiotic factors change, the composition of plant and animal communities also changes.

Patterns of Species Distribution

Ecologists who study biogeography examine patterns of species distribution. No species exists everywhere; for example, the Venus flytrap is endemic to a small area in North and South Carolina. An **endemic species** is one that is naturally found only in a specific geographic area that is usually restricted in size. Other species are **cosmopolitan**: species that live in a wide variety of geographic areas; the raccoon, for example, is native to most of North and Central America.

Since species distribution patterns are based on biotic and abiotic factors and their influences during the very long periods of time required for species evolution, early studies of biogeography were closely linked to the emergence of evolutionary thinking in the eighteenth century. Some of the most distinctive assemblages of plants and animals occur in regions that have been physically separated for millions of years by geographic barriers. Biologists estimate that Australia, for example, has between 600,000 and 700,000 species of plants and animals. Approximately 3/4 of living plant and mammal species are endemic species found solely in Australia.



Figure 3.2.14: Australia is home to many endemic species. The (a) wallaby (*Wallabia bicolor*), a medium-sized member of the kangaroo family, is a pouched mammal, or marsupial. The (b) echidna (*Tachyglossus aculeatus*) is an egg-laying mammal.

The geographic distribution of organisms on the planet follows patterns that are best explained by evolution in conjunction with the movement of tectonic plates over geological time. Broad groups that evolved before the breakup of the supercontinent Pangaea (about 200 million years ago) are distributed worldwide. Groups that evolved since the breakup appear uniquely in regions of the planet, such as the unique flora and fauna of northern continents that formed from the supercontinent Laurasia and of the southern continents that formed from the supercontinent Gondwana. The presence of *Glossopteris* in Australia, Antarctica, India, Africa, and South America is best explained by the plant family's presence there prior to the southern supercontinent Gondwana breaking up.

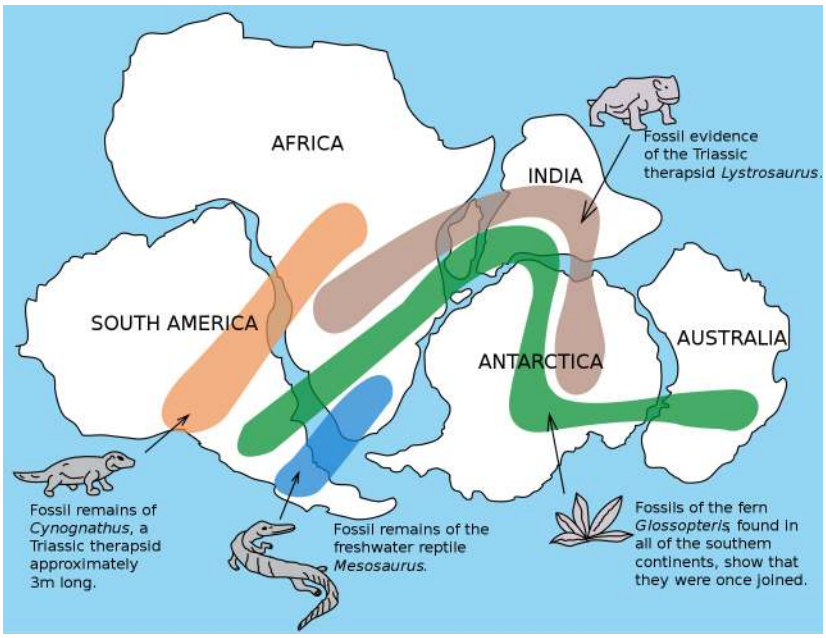


Figure 3.2.15: The *Glossopteris* genus of ferns evolved before the supercontinent Gondwana broke up. Today, members of this plant family are found throughout the southern hemisphere (shown in green).

Artificial Selection: Human-Initiated Change

Most contemporary evolutionary biologists study evolution experimentally using laboratory organisms such as *Drosophila* or natural systems in the wild. However, 18th- and 19th-century evolutionary biologists, including Darwin, emphasized the similarities between natural evolution and artificial ‘ improvement’ of livestock under domestication. They believed that studying domesticated animals and plants could illuminate the mechanisms of natural evolution. Indeed, Chapter 1 of *On the Origin of Species…* is entitled ‘Variation under domestication’. Recent discoveries reveal the relationship between natural evolutionary mechanisms and the practical technologies used to breed plants, animals, yeasts, and microbes, to produce food, clothing, transport, companionship, decoration, entertainment, and medicines.

Artificial selection is any selective breeding intentionally practiced by humans leading to the evolution of domesticated organisms. Artificial selection may oppose or amplify or be neutral in relation to natural selection. Most livestock, including dogs, cats, goats, pigs, cattle, sheep, guinea pigs, horses, geese, poultry, and scores of crop plants were domesticated more than 5000 years ago. Estimates of dates of domestication based upon the archeological record differ enormously from those based on genetic analysis for almost all crops and livestock. However, experts agree that dogs were among the first mammalian species to become domesticated, followed by sheep. During the last few hundred years, people have domesticated a wide range of other animals such as guppies, hamsters, mice, and budgerigars, mostly for use as pets, together with thousands of culinary, medicinal, and ornamental plants.

Domesticated animals are usually held in small, isolated populations with limited opportunities for interbreeding. For centuries, drovers herded large numbers of non-breeding pigs, cattle, sheep, geese, and poultry to market for slaughter, often over hundreds of kilometers. However, the breeding stocks were usually kept within a small area because moving sexually active bulls and large boars over long distances was much less practical. It is important to note that true domestication is different from the taming of wild animals. Certain individuals of many species, especially juveniles and females, can be tamed and live in captivity where they are protected from predators and provided with food and shelter. Domesticated livestock are also fed and protected, but many generations breed and spend their entire lives in close association with humans.

For centuries, livestock breeders have nurtured strains of animals that thrive on various diets or in particular climates or that excel in certain roles. Sometimes, the domestication was simply due to the whims of the breeder. The variety of such animals seems bewildering but certain changes consistently emerge in a surprisingly wide range of domesticated species and among humans, suggesting that similar mechanisms are operating.

Videos



This 5-minute video explains the current hypothesis for the origins of the modern dog.
Question after watching: Human-initiated selection is a large influence on the evolution of modern dogs. What role did natural selection also play?



This 6-minute video describes how broccoli, cabbage, and kohlrabi are all varieties of the same species.
Question after watching: You go to the garden centre and obtain a few strawberry plants. You want to breed the sweetest berries. How would you go about obtaining such a berry? Link each step to a similar step in the process of natural selection.

Parts adapted from ("Evolution: artificial selection and domestication"; CC BY-NC-SA 2.0 UK)

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3.2.1: Scientist Spotlight - Ynes Enriquetta Julietta Mexia

Ynes Enriquetta Julietta Mexia 3.2.1.1

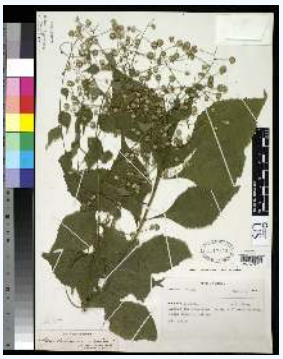
When retracing the history of ecology, it is easy to come to a full-stop at Charles Darwin's *On the Origin of Species*. His theory of evolution by natural selection shook the scientific community to its core, and observations used to synthesize this theory were collected on a five-year voyage around the world. However, Darwin was not the only one to achieve an expedition of such grandiose scale.

Motivated by a newfound interest in science, Ynes Enriquetta Mexia enrolled in classes at UC Berkeley in 1921. She was 51 years old at the time. By the age of 55, she was engaged in a series of botanical expeditions in remote Alaska and in South/Central America. Alongside a Stanford University botanist, Mexia collected 500 plant specimens on her first trip to Mexico. She went on to collect about 145,000 specimens over the next 13 years, 500 of which were new species. Charles Darwin collected a mere 500 specimens on his famed five-year voyage. In addition to the sheer number of Mexia's samples, she was a natural scientist whose research contributed immensely to the modern classification of plants in North America. Her "discoveries helped to clarify and complete botanical records."



Figure 1: Ynes Mexia. Source: https://en.wikipedia.org/wiki/Ynes_M...Ynes_Mexia.jpg

Despite her impressive fieldwork, Mexia never received recognition comparable to that of her male counterparts. However, of the 500 plant species she discovered, 50 were named after her, as well as the entire genus *Mexianthus*.



A *Mexianthus mexicanus* specimen collected by Ynes E. J. Mexia. This photo, from the Smithsonian Institution, is in the Public Domain.

Sources

Spotlight inspiration from the Scientist Spotlights Initiative

Elias, Sarah. Ynes Enriquetta Julietta Mexia. <scientistspotlights.org/scientist/ynes-enriquetta-julietta-mexia/>. Accessed September 21, 2021.

Smithsonian Institution. Mexianthus mexicanus B.L. Rob. <https://www.si.edu/object/mexianthus-mexicanus-bl-rob%3Anmnhbotany_2150513>. Accessed September 21, 2021.

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Natural Selection and Adaptive Evolution

- Please read and watch the following Mandatory Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 1.5 hours.
- Optional Activities are embedded.
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  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Explain how natural selection leads to adaptive evolution
- Contrast stabilizing selection, directional selection, and diversifying selection.
- Describe frequency-dependent selection
- Explain the effects of sexual dimorphism on the reproductive potential of an organism

Introduction to Natural Selection

Natural selection drives adaptive evolution by selecting for and increasing the occurrence of beneficial traits in a population. Natural selection only acts on the population's heritable traits: selecting for beneficial alleles and, thus, increasing their frequency in the population, while selecting against deleterious alleles and, thereby, decreasing their frequency. This process is known as **adaptive evolution** (Figure 3.3.1). Natural selection does not act on individual alleles, however, but on entire organisms. An individual may carry a very beneficial genotype with a resulting phenotype that, for example, increases the ability to reproduce. If that same individual also carries an allele that results in a fatal childhood disease, however, the fecundity phenotype will not be passed on to the next generation because the individual will not live to reach reproductive age. Natural selection acts at the level of the individual. It selects for individuals with greater contributions to the gene pool of the next generation, known as an organism's **evolutionary fitness**.

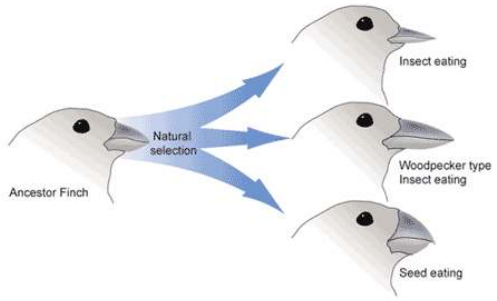


Figure 3.3.1: Through natural selection, a population of finches evolved into three separate species by adapting to several different selection pressures. Each of the three modern finches has a beak adapted to its life history and diet.

Evolutionary fitness is often quantifiable as the contribution of genetic information by an individual to subsequent generations. However, it is not the absolute fitness of an individual that counts, but rather how it compares to the other organisms in the population. This concept, called **relative fitness**, allows researchers to determine which individuals are contributing additional offspring to the next generation and, thus, how the population might evolve.

Genetic Variation and Natural Selection

Natural selection and some of the other evolutionary forces can only act on heritable traits, namely an organism's genetic code. Because alleles are passed from parent to offspring, those that confer beneficial traits or behaviors may be selected for, while deleterious alleles may be selected against. Acquired traits, for the most part, are not heritable. For example, if an athlete works out in the gym every day, building up muscle strength, the athlete's offspring will not necessarily grow up to be a bodybuilder. If there is a genetic basis for the ability to run fast, on the other hand, this may be passed to a child.

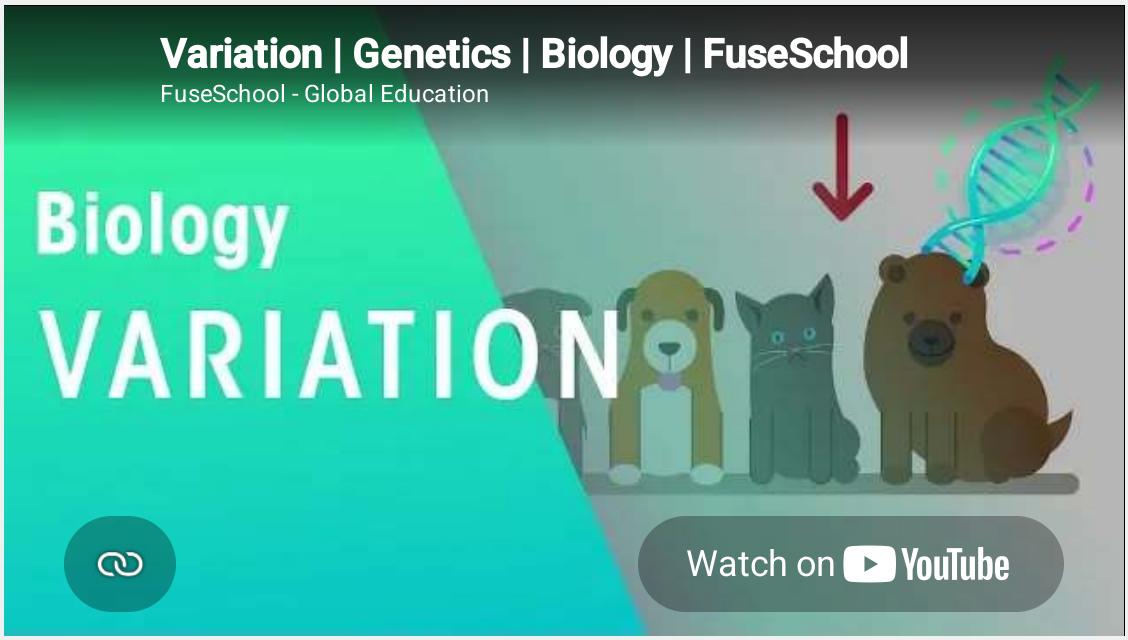
Genetic variation is a measure of the genetic differences (diversity of alleles and genotypes) that exist within a population. The genetic variation of an entire species is often called genetic diversity. Genetic variations are the differences in DNA segments or genes between individuals and each variation of a gene is called an allele. For example, a population with many different alleles at a single chromosome locus has a high amount of genetic variation. Genetic variation is essential for natural selection because natural selection can only increase or decrease the frequency of alleles that already exist in the population.

Genetic variation is caused by:

- mutation (discussed further in Section 2.2.4)
- random mating between organisms (discussed further in Section 2.2.4)
- random fertilization
- genetic recombination during meiosis

Mutations are the only method of creating new alleles; mutations are ultimately the engine that drives evolution. Sexual reproduction (including random mating, random fertilization, and crossing over) are ways to reshuffle and recombine those genes in new ways, giving offspring combinations that differ from their parents and from others.

Video





This 4-minute video provides a brief introduction to variation in humans and a method for identifying traits that are encoded by genetics and those determined by the environment.

Question after watching:

In most cases, when a person who has an identical two develops a disease like cancer, their identical twin does not. What does this tell you about the causes of cancer?

Evolution and Adaptation to the Environment

Variation allows some individuals within a population to adapt to the changing environment. Because natural selection acts directly only on phenotypes, more genetic variation within a population usually enables more phenotypic variation. Some new alleles increase an organism's ability to survive and reproduce, which then ensures the survival of the allele in the population. Other new alleles may be immediately detrimental (such as a malformed oxygen-carrying protein) and organisms carrying these new mutations will die out. Neutral alleles are neither selected for nor against and usually remain in the population. Genetic variation is advantageous because it enables some individuals and, therefore, a population, to survive despite a changing environment (Figure 3.3.2).



Figure 3.3.2: Populations of wild cheetahs have very low genetic variation. Because wild cheetahs are threatened, their species has a very low genetic diversity. This low genetic diversity means they are often susceptible to disease and often pass on lethal recessive mutations; only about 5% of cheetahs survive to adulthood.

Geographic Variation

Some species display geographic variation as well as variation within a population. Geographic variation, or the distinctions in the genetic makeup of different populations, often occurs when populations are geographically separated by environmental barriers or when they are under selection pressures from a different environment. One example of geographic variation are **clines**, gradual changes in a trait across an organism's geographic distribution.

Species of warm-blooded animals, for example, tend to have larger bodies in the cooler climates closer to the earth's poles, allowing them to better conserve heat. This is considered a *latitudinal cline* (Figure 3.3.3). Alternatively, flowering plants tend to bloom at different times depending on where they are along the slope of a mountain, known as an *altitudinal cline*.

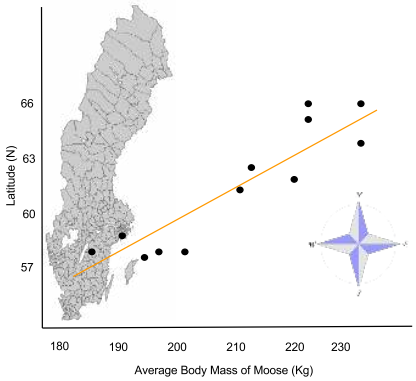


Figure 3.3.3: This graph shows geographical variation in moose; body mass increase positively with latitude. Bergmann's Rule is an ecologic principle that states that as latitude increases the body mass of a particular species increases. The data are taken from a Swedish study investigating the size of moose as latitude increases as shows the positive relationship between the two, supporting Bergmann's Rule.

Environmental Variance

Genes are not the only players involved in determining population variation. Phenotypes are also influenced by other factors, such as the environment (Figure 3.3.4). Some major characteristics, such as gender, are determined by the environment for some species. For example, some turtles and other reptiles have temperature-dependent sex determination (TSD). TSD means that individuals develop into males if their eggs are incubated within a certain temperature range, or females at a different temperature range.



Figure 3.3.4: The sex of the American alligator (*Alligator mississippiensis*) is determined by the temperature at which the eggs are incubated. Eggs incubated at 30°C produce females, and eggs incubated at 33°C produce males. (credit: Steve Hillebrand, USFWS)

Types of Natural Selection

There are several ways selection can affect population variation (each is described in detail below):

- stabilizing selection
- directional selection
- diversifying selection
- frequency-dependent selection
- sexual selection

As natural selection influences the traits in a population, individuals can either become more or less genetically similar to one another and the phenotypes displayed can become more similar or more disparate. In the end, natural selection cannot produce perfect organisms from scratch, it can only generate populations that are better adapted to survive and successfully reproduce in their environments through the aforementioned selections.

Video





In this 3-minute video, David Attenborough explains how iguana evolved to swim on the Galpagos islands.
Question after watching:
Propose a series of steps that could have led to this evolution in the iguana population in the Galpagos. Specifically, explain how they evolved to live for short periods underwater from their land ancestor.

Stabilizing, Directional, and Diversifying Selection

Stabilizing Selection

If natural selection favors an average phenotype by selecting against extreme variation, the population will undergo stabilizing selection.



Stabilizing selection: Stabilizing selection occurs when the population stabilizes on a particular trait value and genetic diversity decreases. In the graph above, the x-axis indicates the variation in a trait. The y-axis indicates the percentage of individuals in a population that have a particular trait. In stabilizing selection, the average becomes more common over time, with less variation in the population.

For example, in a population of mice that live in the woods, natural selection will tend to favor individuals that best blend in with the forest floor and are less likely to be spotted by predators. Assuming the ground is a fairly consistent shade of brown, those mice whose fur most closely matches that color will most probably survive and reproduce, passing on their genes for their brown coat. Mice that carry alleles that make them slightly lighter or slightly darker will stand out against the ground and will more probably die from predation. As a result of this stabilizing selection, the population's genetic variance will decrease.

Directional Selection

When the environment changes, populations will often undergo directional selection, which selects for phenotypes at one end of the spectrum of existing variation.



Directional selection: Directional selection occurs when a single phenotype is favored, causing population to shift towards one end of the trait variation. In the graph above, the x-axis indicates the variation in a trait. The y-axis indicates the percentage of individuals in a population that have a particular trait. In directional selection, the average shifts one direction or another but the total variation in the population remains.

A classic example of this type of selection is the evolution of the peppered moth (*Biston betularia*) in eighteenth- and nineteenth-century England. Prior to the Industrial Revolution, the moths were predominately light in color, which allowed them to blend in with the light-colored trees and lichens in their environment. As soot began spewing from factories, the trees darkened and the light-colored moths became easier for predatory birds to spot.

Over time, the frequency of the melanic (dark) form of the moth increased because their darker coloration provided camouflage against the sooty tree; they had a higher survival rate in habitats affected by air pollution (Figure 3.3.5). Similarly, a hypothetical mouse population may evolve to take on a different coloration if their forest floor habitat changed. The result of this type of selection is a shift in the population's genetic variance toward the new, fit phenotype.



Figure 3.3.5: Two morphs of the peppered moth (*Biston betularia*) resting on the same tree. The light-colored typical moroph (below the bark's scar) is nearly invisible on this pollution-free tree, camouflaging it from predators while the carbonaria morph stands out clearly.

Diversifying (or Disruptive) Selection

Sometimes natural selection can select for two or more distinct phenotypes that each have their advantages. In these cases, the intermediate phenotypes are often less fit than their extreme counterparts.

disruptive selection

Diversifying (or disruptive) selection: Diversifying selection occurs when extreme values for a trait are favored over intermediate values. This type of selection often drives speciation. In the graph above the x-axis indicates the variation in a trait. The y-axis indicates the percentage of individuals in a population that have a particular trait. In directional selection, the average is selected against, leading to selection for the rarer variations of a trait.

This is seen in many populations of animals that have multiple male mating strategies, such as lobsters. Large, dominant alpha males obtain mates by brute force, while small males can sneak in for furtive copulations with the females in an alpha male's territory. In this case, both the alpha males and the "sneaking" males will be selected for, but medium-sized males, which cannot overtake the alpha males and are too big to sneak copulations, are selected against.

Diversifying selection can also occur when environmental changes favor individuals on either end of the phenotypic spectrum. Imagine a population of mice living at the beach where there is light-colored sand interspersed with patches of tall grass. In this scenario, light-colored mice that blend in with the sand would be favored, as well as dark-colored mice that can hide in the grass. Medium-colored mice, on the other hand, would not blend in with either the grass or the sand and, thus, would more probably be eaten by predators. The result of this type of selection is increased genetic variance as the population becomes more diverse.

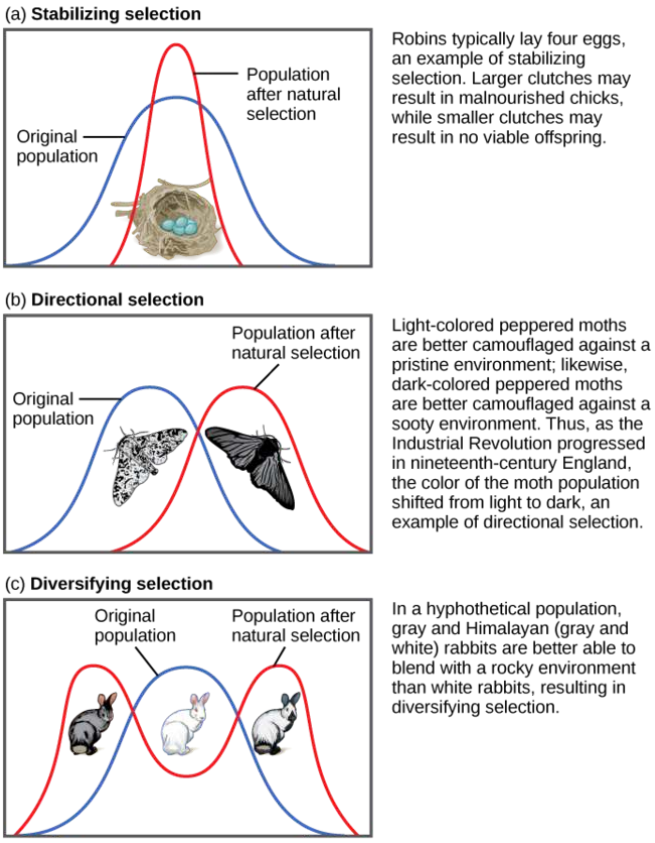
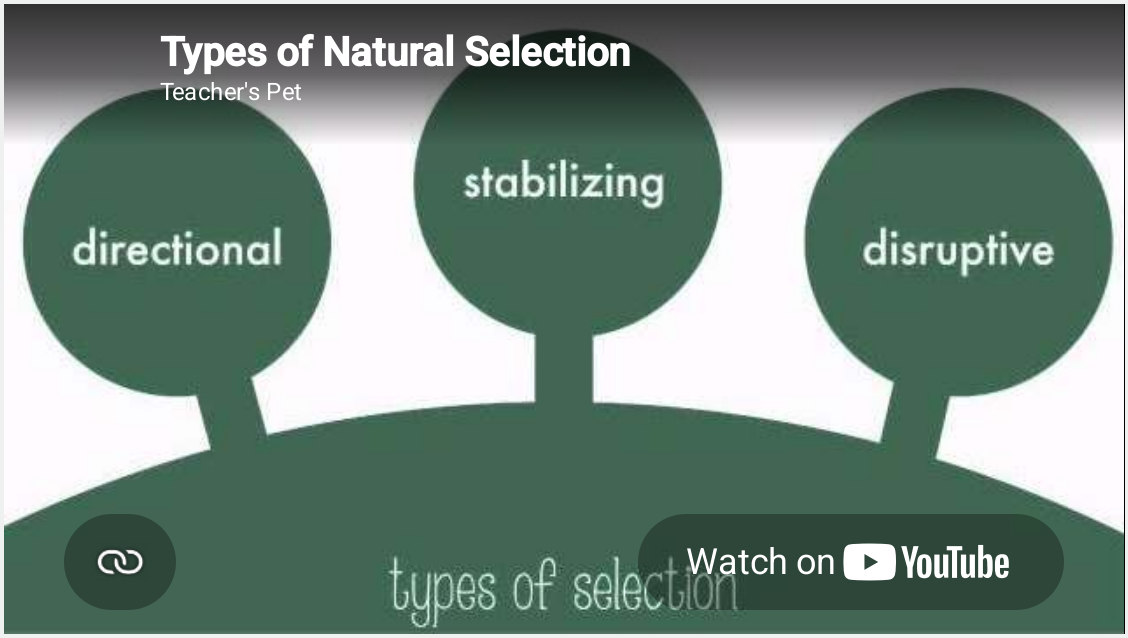
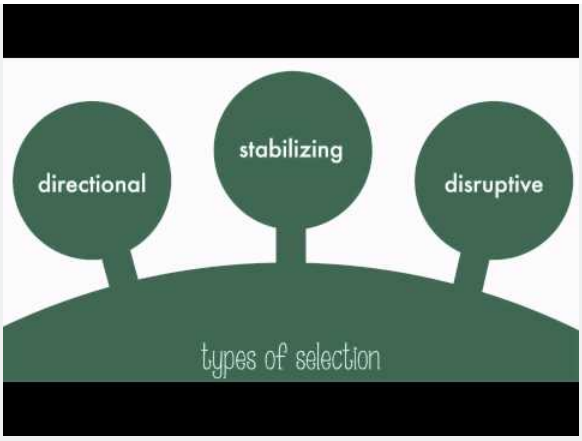


Figure 3.3.6: Different types of natural selection can impact the distribution of phenotypes within a population. In (a) stabilizing selection, an average phenotype is favored. In (b) directional selection, a change in the environment shifts the spectrum of phenotypes observed. In (c) diversifying selection, two or more extreme phenotypes are selected for, while the average phenotype is selected against.

Video





This 2.5-minute video highlights directional, stabilizing, and disruptive selection.
Question after watching:
In the video, the narrator speaks of disruptive selection (this textbook called it diversifying selection). What is being disrupted?

Frequency-Dependent Selection

Another type of selection, called **frequency-dependent selection**, favors phenotypes that are either common (positive frequency-dependent selection) or rare (negative frequency-dependent selection).

Negative Frequency-Dependent Selection

Negative frequency-dependent selection increases the population's genetic variance by selecting for rare phenotypes. An interesting example of this type of selection is seen in a unique group of lizards in the deserts of the United States. Male common side-blotched lizards come in three throat-color patterns: orange, blue, and yellow. Each of these forms has a different reproductive strategy: orange males are the strongest and can fight other males for access to their females; blue males are medium-sized and form strong pair bonds with their mates; and yellow males are the smallest and look a bit like female, allowing them to sneak copulations.

Like a game of rock-paper-scissors, orange beats blue, blue beats yellow, and yellow beats orange in the competition for females. The big, strong orange males can fight off the blue males to mate with the blue's pair-bonded females; the blue males are successful at guarding their mates against yellow sneaker males; and the yellow males can sneak copulations from the potential mates of the large, polygynous orange males (Figure 3.3.7).

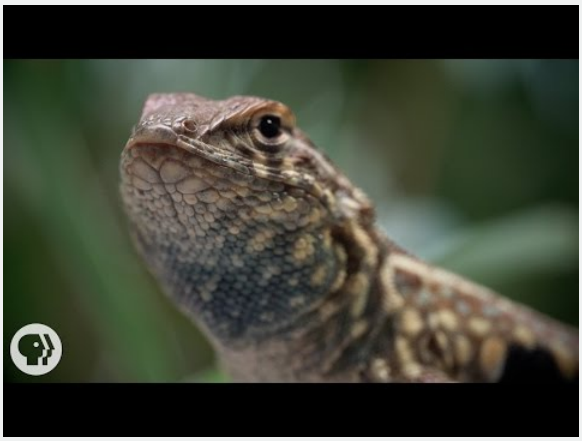
In this scenario, orange males will be favored by natural selection when the population is dominated by blue males, blue males will thrive when the population is mostly yellow males, and yellow males will be selected for when orange males are the most populous. As a result, populations of side-blotched lizards cycle in the distribution of these phenotypes. In one generation, orange might be predominant and then yellow males will begin to rise in frequency. Once yellow males make up a majority of the population, blue males will be selected for. Finally, when blue males become common, orange males will once again be favored. So, orange (strong) > blue (cooperation) > yellow (sneaky) > orange (strong).



Figure 3.3.7: A yellow-throated side-blotched lizard (seen here) is smaller than either the blue-throated or orange-throated males and appears a bit like the females of the species, allowing it to sneak copulations. Frequency-dependent selection allows for both common and rare phenotypes of the population to appear in a frequency-aided cycle.

Video





This 3.5-minute video illustrates the side-blotched lizard case study of negative frequency-dependent selection.

Question after watching:

The video mentions that the blues can be altruistic, which is to say exhibit behaviour that would benefit not themselves but another animal. Propose a hypothesis about the evolutionary advantage of altruism in this case.

Positive Frequency-dependent Selection

Positive frequency-dependent selection usually decreases genetic variance by selecting for common phenotypes. An example of positive frequency-dependent selection is the mimicry of the warning coloration of dangerous species of animals by other species that are harmless.

The scarlet kingsnake (*Lampropeltis elapsoides*), a harmless species, mimics the coloration of the eastern coral snake *(Micrurus fulvius),* a venomous species typically found in the same geographical region (Figure 3.3.8). Predators learn to avoid both species of snake due to the similar coloration. As a result, the scarlet kingsnake becomes more common and its coloration phenotype becomes more variable due to relaxed selection. This phenotype is, therefore, more “fit” as the population of species that possess it (both dangerous and harmless) becomes more numerous. In geographic areas where the coral snake is less common, the pattern becomes less advantageous to the kingsnake, and much less variable in its expression, presumably because predators in these regions are not “educated” to avoid the pattern.



Figure 3.3.8 : The scarlet kingsnake (*Lampropeltis elapsoides*), left, mimics the coloration of the poisonous eastern coral snake (Micrurus fulvius), right. Positive frequency-dependent selection reinforces the common phenotype because predators avoid the distinct coloration. The eastern coral snake (Micrurus fulvius)is venomous and advertises this through its coloring.





In this short 1-minute narrated by David Attenborough, you will see several examples of biomimicry, where animals evolved shapes and colors that make them look like something else.

Question after watching:

What appears to be the purpose of biomimicry in most organisms? At which step in a process of natural selection would the mimicry provide an advantage?

Sexual Selection

Sexual selection, the selection pressure on males and females in mating, can result in traits designed to maximize sexual success. In species with sexual selection, typically one sex is less-limited due to their ability to produce an overabundance of gametes and the other is more-limited due to their higher parental investment (e.g. produce eggs, gestate a fetus, raise young, etc.). The more-limited sex typically reproduces fewer times and has higher parental investment than the less-limited sex; they are typically more discerning about who they mate with in order to optimize those reproductive events.

Sexual selection in animals takes two major forms: **intersexual selection** in which, the less-limited sex (typically males) are chosen by the more-limited sex (typically females) based on certain characteristics and **intrasexual selection** in which members of the less-limited sex compete aggressively among themselves for access to the more-limited sex (Figure 3.3.9).



Figure 3.3.9: This male elk has large antlers to compete with rival males for available females (intrasexual competition). In addition, the many points on his antlers represent health and longevity, and therefore he may be more desirable to females (intersexual selection).

Video





This 3-minute video highlights extreme behaviors that arise from intense sexual selection pressure.

Question after watching:

What can you surmise about which of the sexes are 'choosier' in most mammals, based on morphological and behavioural dimorphism?

Sexual Dimorphism in Animals

Males and females of certain animal species are often quite different from one another in ways beyond the reproductive organs. Male vertebrates are often larger, for example, and display many elaborate colors, adornments, and behaviors such as seen in the figure below, while females of the same species tend to be smaller and less attention-seeking. These differences are called **sexual dimorphisms** and arise from the variation in reproductive success (Figure 3.3.10).

Animal females do not have trouble finding mates for reproduction, while reproduction is not guaranteed for males. The bigger, stronger, or more decorated males usually obtain the vast majority of the total reproductive events, while other males receive none. This can occur because the males are better at fighting off other males (intrasexual selection), or because females will choose to mate with the bigger, brasher, or more decorated males (intersexual selection). In either case, this variation in reproductive success generates a strong selection pressure among males to compete for mates, resulting in the evolution of bigger body sizes or elaborate ornaments in order to increase their chances of mating. Females, on the other hand, tend to get a handful of selected matings; therefore, they are more likely to be selective in their mates.



Figure 3.3.10: Morphological differences between males and females of the same species is known as sexual dimorphism. These differences can be observed in (a) peacocks and peahens, (b) *Argiope appensa* spiders (the female spider is the large one), and (c) wood ducks.

Sexual dimorphism varies widely among species; some species are even sex-role reversed. In such cases, females tend to have a greater variation in their reproductive success than males and are, correspondingly, selected for the bigger body size and elaborate traits usually characteristic of males.

The Handicap Principle

Sexual selection can be so strong that it selects for traits that are actually detrimental to the individual's survival because they maximize its reproductive success. For example, while the male peacock's tail is beautiful, and the male with the largest, most colorful tail will more probably win a female's attention, it is not practical or advantageous (Figure 3.3.11). In addition to making the males more visible to predators, it slows down any needed escapes. There is some evidence that this risk is why females like the big, bright tails. Because large tails carry risk, only the best males can survive that risk, and therefore the bigger the tail the more fit the male must be. This idea is known as the **handicap principle**.



Figure 3.3.11: This male ribbon-tailed astrapia, *Astrapia mayeri*, a bird of paradise, carries an extremely long tail as the result of sexual selection. The tail is flamboyant and detrimental to the bird's own survival, but it increases his reproductive success. This may be an example of the handicap principle.

The Good Genes Hypothesis

The **good genes hypothesis** states that males develop these impressive ornaments to show off their efficient metabolism or their ability to fight disease. Females then choose males with the most impressive traits because it signals their genetic superiority, which they will then pass on to their offspring. Though it might be argued that females should not be so selective because it will likely reduce their number of offspring, if better males father more fit offspring, it may be beneficial. Fewer, healthier offspring may increase the chances of survival more than many, weaker offspring.

Video





This 8.5-minute video is an overview of natural and sexual selection.

Questions after watching:

How is sexual selection an example or type of natural selection? Explain the following statement: "evolution is just a numbers game"

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3.4: Additional Mechanisms of Evolution

Additional Mechanisms of Evolution

- Please read and watch the following Mandatory Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 2 hours.
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Learning Objectives

- Identify the four agents of evolutionary change other than natural selection
- Explain genetic drift, including the bottleneck and founder effects
- Describe gene flow and how it maintains genetic variance in a population
- Explain how each evolutionary force can influence the allele frequencies of a population

In addition to natural selection, there are four other agents of evolutionary change: mutation, genetic drift, gene flow, and non-random mating. These serve to either increase or decrease genetic variation in the population. Mutations are changes to an organism's DNA and are an important driver of diversity in populations. Genetic drift is the impact on a population's genetic variance due to random chance events, such as natural disasters. Gene flow is the exchange of genetic information between populations and serves to keep disparate populations more similar to one another. Nonrandom mating describes the process of "choice" within reproduction based on perceived evolutionary fitness. Each of these additional agents is discussed below in concert with natural selection as none of these forces acts in isolation.

Four Additional Agents of Evolutionary Change

1. Mutation

Species ultimately evolve because of the accumulation of mutations that occur over time. The appearance of new mutations is the most common way to introduce novel genotypic and phenotypic variance (Figure 3.4.1). Without new mutations, genetic variance in a population would lessen over time in stable environmental conditions (stabilizing selection) leading populations to be less able to survive future changes. Mutations can only influence evolution if they are heritable (e.g. carried within the gametes).

Some mutations are unfavorable or harmful and are quickly eliminated from the population by natural selection as see in Figure 3.4.2. Others are beneficial and will spread through the population. Whether or not a mutation is beneficial or harmful is determined by whether it helps an organism survive to sexual maturity and reproduce. Some mutations do not do anything and can linger, unaffected by natural selection, in the genome (e.g. in the somatic cells). Some can have a dramatic effect on a gene and the resulting phenotype.



Figure 3.4.1: A mutation has caused this garden moss rose to produce flowers of different colors. This mutation has introduced a new allele into the population that increases genetic variation and may be passed on to the next generation.

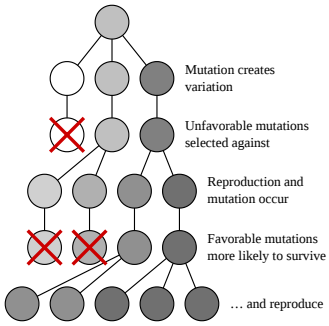
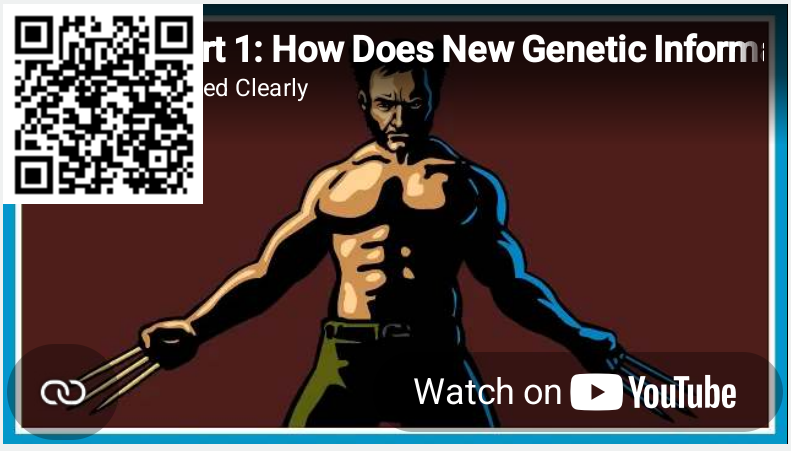


Figure 3.4.2: As mutations create variation, natural selection affects the frequency of that trait in a population. Mutations that confer a benefit (such as running faster or digesting food more efficiently) can help that organism survive and reproduce, carrying the mutation to the next generation.

Video



This 7-minute video provides an overview of DNA mutations and their impact on the proteins they encode and the phenotype of an organism.

Question after watching:

If a mutation does not impact an organism's phenotype, and this mutation is found over time to increase in a population, does this constitute evolution? If so, what is the likely cause of this evolution?

2. Genetic Drift

Another way a population's allele and genotype frequencies can change is **genetic drift**, which is simply the effect of chance on the population's genetic variation. For example, some individuals will have more offspring than others—not due to an advantage conferred by some genetically-encoded trait, but just because one male happened to be in the right place at the right time (when the receptive female walked by) or because the other one happened to be in the wrong place at the wrong time (when a fox was hunting).

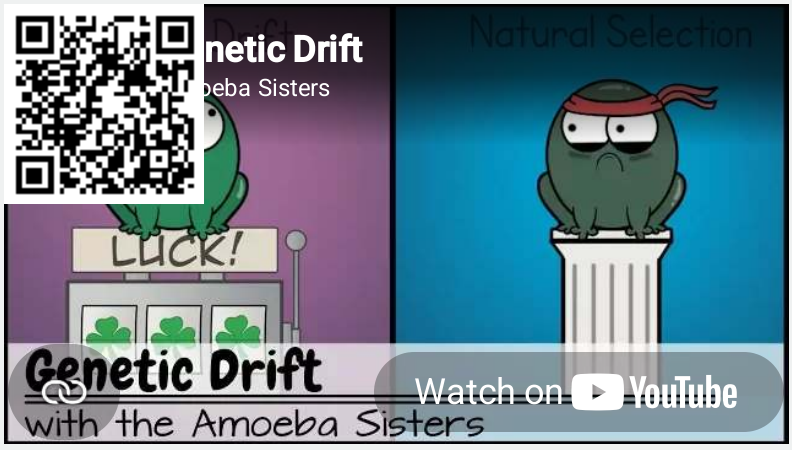
Genetic Drift vs. Natural Selection

Genetic drift is the opposite of natural selection. The theory of natural selection maintains that some individuals in a population have traits that enable them to survive and produce more offspring, while other individuals have traits that are detrimental and may cause them to die before reproducing. Over successive generations, these selection pressures can change the gene pool and the traits within the population. For example, a big, powerful male gorilla will mate with more females than a small, weak male and therefore more of his genes will be passed on to the next generation. His offspring may continue to dominate the troop and pass on their genes as well. Over time, the selection pressure will cause the allele frequencies in the gorilla population to shift toward large, strong males.

Unlike natural selection, genetic drift describes the effect of chance on populations in the absence of positive or negative selection pressure. Through random sampling or the survival or reproduction of a random sample of individuals within a population, allele frequencies within a population may change. Rather than a male gorilla producing more offspring because he is stronger, he may be the only male available when a female is ready to mate. His genes are passed on to future generations because of chance, not because he was the biggest or the strongest. Genetic drift is the shift of alleles within a population due to chance events that cause random samples of the population to reproduce or not.

Small populations are more susceptible to the forces of genetic drift. Large populations, on the other hand, are buffered against the effects of chance. If one individual of a population of 10 individuals happens to die at a young age before leaving any offspring to the next generation, all of its genes (1/10 of the population's gene pool) will be suddenly lost. In a population of 100, that individual represents only 1 percent of the overall gene pool; therefore, genetic drift has much less impact on the larger population's genetic structure.

Video



This 4.5-minute video describes how genetic drift occurs by chance.

Question after watching:

Describe a situation in which a population would undergo the bottleneck effect and explain what impact that would have on the population's genetic variance.

The Bottleneck Effect

Genetic drift can be magnified by natural events, such as a natural disaster that kills a large portion of the population at random. This **bottleneck effect** occurs when only a few individuals survive and reduce variation in the gene pool of a population (Figure

3.4.3). The genetic structure of the survivors becomes the genetic structure of the entire population, which may be very different from the pre-disaster population.

Captive breeding programs can fall victim to the bottleneck effect when species are at endangered or threatened levels. When scientists are involved in the breeding of a species, such as with animals in zoos and nature preserves, they try to increase a population's genetic variance to preserve as much of the phenotypic diversity as they can. This also helps reduce the risks associated with inbreeding, the mating of closely related individuals, which can have the undesirable effect of bringing together deleterious recessive mutations that can cause abnormalities and susceptibility to disease.

For example, a disease that is caused by a rare, recessive allele might exist in a population, but it will only manifest itself when an individual carries two copies of the allele. Because the allele is rare in a normal, healthy population with unrestricted habitat, the chance that two carriers will mate is low, and even then, only 25 percent of their offspring will inherit the disease allele from both parents. While it is likely to happen at some point, it will not happen frequently enough for natural selection to be able to swiftly eliminate the allele from the population, and as a result, the allele will be maintained at low levels in the gene pool. However, if a family of carriers begins to interbreed with each other, this will dramatically increase the likelihood of two carriers mating and eventually producing diseased offspring, a phenomenon known as inbreeding depression.

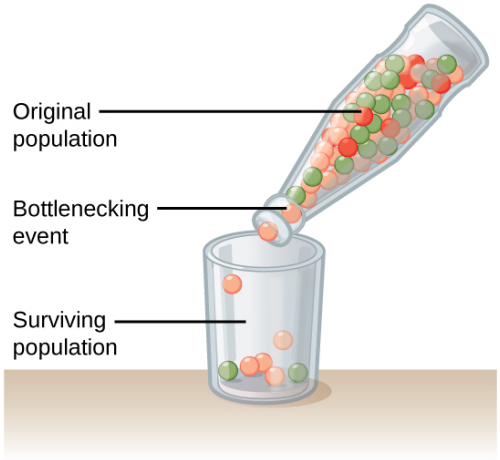


Figure 3.4.3: A chance event or catastrophe can reduce the genetic variability within a population.

The Founder Effect

Another scenario in which populations might experience a strong influence of genetic drift is if some portion of the population leaves to start a new population in a new location or if a population gets divided by a physical barrier of some kind (Figure 3.4.4). In this situation, it is improbable that those individuals are representative of the entire population, which results in the **founder effect**. The founder effect occurs when the genetic structure changes to match that of the new population's founding fathers and mothers.

The founder effect is believed to have been a key factor in the genetic history of the Afrikaner population of Dutch settlers in South Africa, as evidenced by mutations that are common in Afrikaners, but rare in most other populations. This was probably due to the fact that a higher-than-normal proportion of the founding colonists carried these mutations. As a result, the population expresses unusually high incidences of Huntington's disease (HD) and Fanconi anemia (FA), a genetic disorder known to cause blood marrow and congenital abnormalities, even cancer.

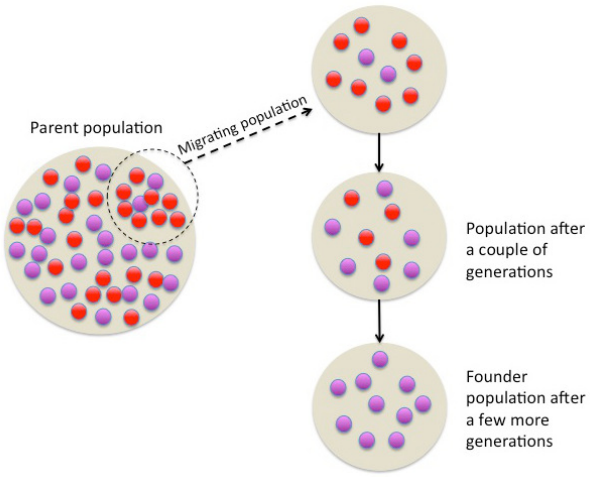
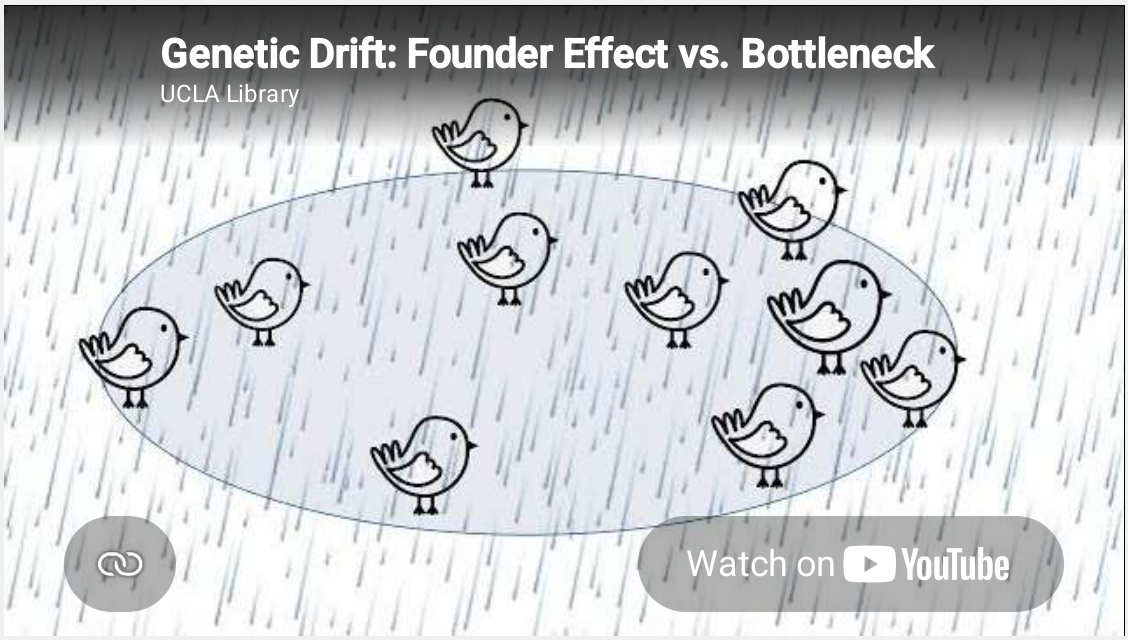
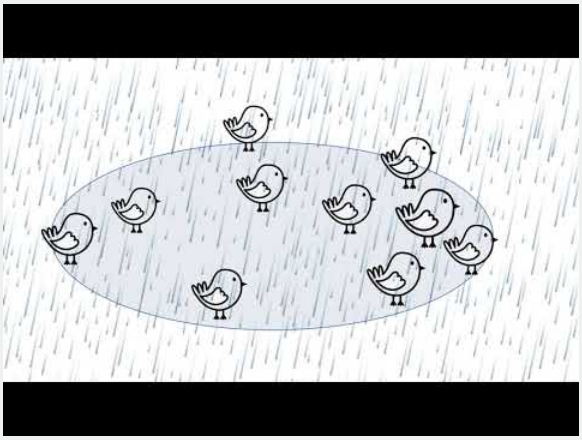


Figure 3.4.4: The founder effect occurs when a portion of the population (i.e. “founders”) separates from the old population to start a new population with different allele frequencies. (Tsaneda; CC-BY-SA 4.0)

Video





This 1-minute video differentiates the founder effect from a bottleneck event, which are similar but different.
Question after watching:
50,000 years ago, a small group of people migrated out of Africa. Their descendants populated Asia, Europe, and the Americas. Which type of event is this: founder or bottleneck?

[Optional Activity] Scientific Method Connection: Testing the Bottleneck Effect

Question: How do natural disasters affect the genetic structure of a population?

Background: When much of a population is suddenly wiped out by an earthquake or hurricane, the individuals that survive the event are usually a random sampling of the original group. As a result, the genetic makeup of the population can change dramatically. This phenomenon is known as the bottleneck effect.

Hypothesis: Repeated natural disasters will yield different population genetic structures; therefore, each time this experiment is run, the results will vary.

Test the hypothesis: Count out an original parent population of 100 individuals using different colored beads. For example, red, blue, and yellow beads might represent red, blue, and yellow individuals. After recording the number of each individual in the original population, place them all in a bottle with a narrow neck that will only allow a few beads out at a time. Then, pour approximately 33 beads into a bowl. This represents the surviving individuals after a natural disaster kills a majority (67%) of the population. Count the number of the different colored beads in the bowl, and record it. Then, place all of the beads back in the bottle and repeat the experiment four more times.

Analyze the data: Compare the five populations that resulted from the experiment. Do the surviving populations all contain the same number of different colored beads or do they vary? Remember, these populations all came from the same exact parent population.

Form a conclusion: Most likely, the five resulting surviving populations will differ quite dramatically. This is because natural disasters are not selective—they kill and spare individuals at random. Now think about how this might affect a real population. What happens when a hurricane hits the Gulf Coast of the United States? How do the seabirds that live on the beach fare?

[Optional] Exercise 3.4.1

Do you think genetic drift would happen more quickly on an island or on the mainland?

Answer

Genetic drift is likely to occur more rapidly on an island where smaller populations are expected to occur.

3. Gene Flow

Another important evolutionary force is **gene flow**: the flow of alleles in and out of a population due to the migration of individuals or gametes (Figure 3.4.5). While some populations are fairly stable, others experience more flux. Many plants, for example, send their pollen far and wide, by wind or by bird, to pollinate other populations of the same species some distance away. Even a population that may initially appear to be stable, such as a pride of lions, can experience its fair share of immigration and emigration as developing males leave their mothers to seek out a new pride with genetically unrelated females. This variable flow of individuals in and out of the group not only changes the gene structure of the population but can also introduce new genetic variation to populations in different geological locations and habitats.

Maintained gene flow between two populations can also lead to a combination of the two gene pools, reducing the genetic variation between the two groups. Gene flow strongly acts against speciation, by recombining the gene pools of the groups, thus repairing the developing differences in genetic variation that would have led to full speciation and creation of daughter species.

For example, if a species of grass grows on both sides of a highway, pollen is likely to be transported from one side to the other and vice versa. If this pollen is able to fertilize the plant where it ends up and produce viable offspring, then the alleles in the pollen have effectively linked the population on one side of the highway with the other.

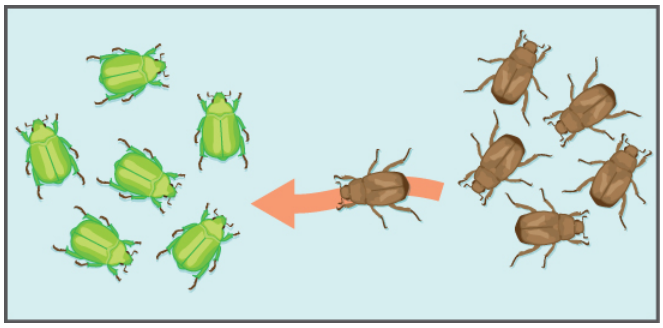


Figure 3.4.5: Gene flow can occur when an individual travels from one geographic location to another.

Video





This video takes the examples of the finches in the Galapagos islands and explains how the different sized beaks on each island resulted from the lack of gene flow between the population on each island.

Question after watching:

Why does the narrator say that in time the different populations that stop having gene flow can become different species. What step needs to happen for this to occur?

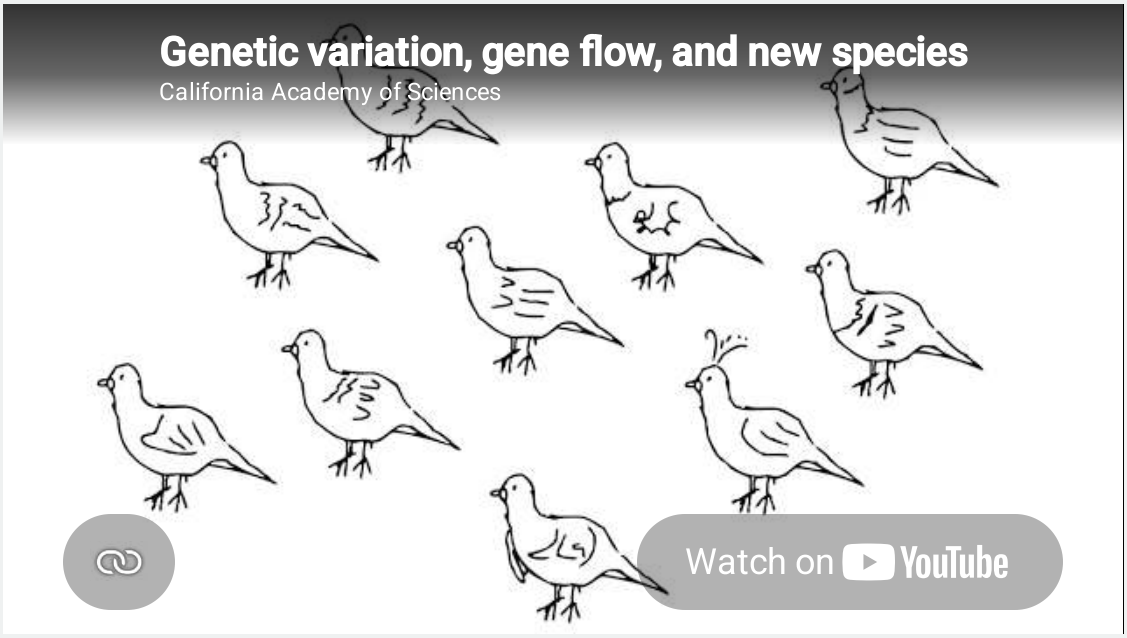
If individuals nonrandomly mate with their peers, the result can be a changing population. There are many reasons nonrandom mating occurs. One reason is simple mate choice; for example, female robins may prefer males with brighter, more orange breast feathers Figure 3.4.6. Traits that lead to more matings for an individual become selected for by natural selection.

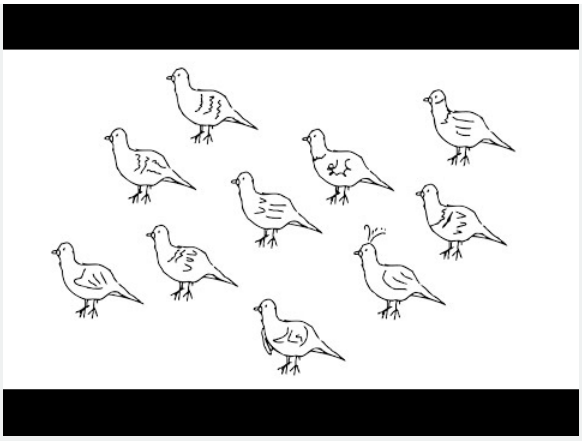
One common form of mate choice, called **assortative mating**, is an individual's preference to mate with partners who are phenotypically similar to themselves. Another cause of nonrandom mating is physical location. This is especially true in large populations spread over large geographic distances where not all individuals will have equal access to one another. Some might be miles apart through woods or over rough terrain, while others might live immediately nearby.



Figure 3.4.6: The American robin (*Turdus migratorius*) may practice assortative mating on plumage color, a melanin-based trait, and mate with other robins who have the most similar shade of color. However, there may also be some sexual selection for more vibrant plumage which indicates health and reproductive performance.

Video





This 12-minute video makes the connection between DNA, mutations, genetic reshuffling through sexual reproduction, and phenotypes/variability between individuals.

Question after watching:

Imagine that the creation of the Panama canal re-opens a route between the two populations of fish presented in the video that had been separated by the landmass. What sort of evolutionary changes would need to happen in either population to lead to specialization?

Footnotes

1. 1 A. J. Tipping et al., “Molecular and Genealogical Evidence for a Founder Effect in Fanconi Anemia Families of the Afrikaner Population of South Africa,” *PNAS* 98, no. 10 (2001): 5734-5739, doi: 10.1073/pnas.091402398.

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CHAPTER OVERVIEW

Chapter 4: Adaptations to the Physical Environment

Learning Objectives

- Describe what an adaptation is and how it arises, and explain examples of common adaptations in plants and animals.
- Compare and contrast some of the broad strategies organisms employ to deal with a variable environment.
- Explain how individual physiological performance can vary with the environment, and link these concepts with population distribution limits and climate change.

4.1: What is adaptation?
4.2: Strategies for dealing with a changing environment

Summary

In biology, adaptation is defined a heritable behavioral, morphological, or physiological trait that has evolved through the process of natural selection, and maintains or increases the fitness of an organism under a given set of environmental conditions. This concept is central to ecology: the study of adaptation is the study of the evolutionary relationship between organisms and their environment. While different groups of plants and animals have adapted to components of their environment in many different ways, more broadly, the two basic solutions for dealing with environmental variation is to conform to the environment or to regulate internal conditions despite the environment. These different strategies influence an organism's physiological performance across variable environmental conditions.

Contributors and Attributions

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4.1: What is adaptation?

Adaptation

In biology, **adaptation** is defined a heritable behavioral, morphological, or physiological trait that has evolved through the process of natural selection, and maintains or increases the fitness of an organism under a given set of environmental conditions. This concept is central to ecology: the study of adaptation is the study of the evolutionary relationship between organisms and their environment.

Adaptation is related to biological fitness, which governs the rate of evolution as measured by change in gene frequencies. Often, two or more species co-adapt and co-evolve as they develop adaptations that interlock with those of the other species, such as with flowering plants and pollinating insects. Features evolved for one purpose may be co-opted for a different one, as when the insulating feathers of dinosaurs were co-opted for bird flight.

History

Adaptation is an observable fact of life accepted by philosophers and natural historians from ancient times, independently of their views on evolution, but their explanations differed.

In natural theology, adaptation was interpreted as the work of a deity and as evidence for the existence of God (Desmond, 1989). Charles Darwin broke with the tradition by emphasizing the flaws and limitations which occurred in the animal and plant worlds (Darwin, 1872). Jean-Baptiste Lamarck proposed a tendency for organisms to become more complex, moving up a ladder of progress, plus "the influence of circumstances," usually expressed as *use and disuse* (Bowler, 1989). This second, subsidiary element of his theory is what is now called Lamarckism, a proto-evolutionary hypothesis of the inheritance of acquired characteristics, intended to explain adaptations by natural means (Bowler, 2003).

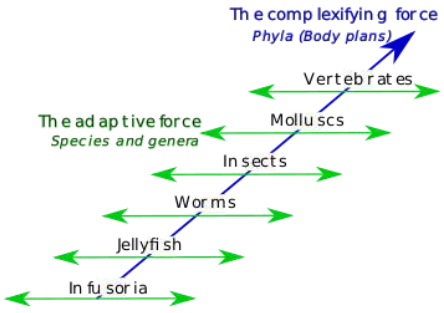


Figure 4.1.1**:** The second of Jean-Baptiste Lamarck's two factors (the first being a complexifying force) was an adaptive force that causes animals with a given body plan to adapt to circumstances by inheritance of acquired characteristics, creating a diversity of species and genera.

Other natural historians, such as Buffon, accepted adaptation, and some also accepted evolution, without voicing their opinions as to the mechanism. This illustrates the real merit of Darwin and Alfred Russel Wallace, and secondary figures such as Henry Walter Bates, for putting forward a mechanism whose significance had only been glimpsed previously. A century later, experimental field studies and breeding experiments by people such as E.B. Ford and Theodosius Dobzhansky produced evidence that natural selection was not only the 'engine' behind adaptation, but was a much stronger force than had previously been thought (Provine, 1986; Ford, 1975; Orr, 2005).

General principles

The significance of an adaptation can only be understood in relation to the total biology of the species.

— Julian Huxley, *Evolution: The Modern Synthesis* (Huxley, 1942)

What adaptation is

Adaptation is primarily a process rather than a physical form or part of a body (Mayr, 1982). An internal parasite (such as a liver fluke) can illustrate the distinction: such a parasite may have a very simple bodily structure, but nevertheless the organism is highly

adapted to its specific environment. From this we see that adaptation is not just a matter of visible traits: in such parasites critical adaptations take place in the life cycle, which is often quite complex (Price, 1980). However, as a practical term, "adaptation" often refers to a *product*: those features of a species which result from the process. Many aspects of an animal or plant can be correctly called adaptations, though there are always some features whose function remains in doubt. By using the term *adaptation* for the evolutionary *process*, and *adaptive trait* for the bodily part or function (the product), one may distinguish the two different senses of the word (Daintith & Martin, 2010; Bowler, 2003; Patterson, 1999; Williams, 1966).

Adaptation is one of the two main processes that explain the observed diversity of species, such as the different species of Darwin's finches. The other process is speciation, in which new species arise, typically through reproductive isolation (Mayr, 1963; Mayr, 1982). An example widely used today to study the interplay of adaptation and speciation is the evolution of cichlid fish in African lakes, where the question of reproductive isolation is complex (Mack et al., 2005; Kornfield & Smith, 2000).

Adaptation is not always a simple matter where the ideal phenotype evolves for a given environment. An organism must be viable at all stages of its development and at all stages of its evolution. This places *constraints* on the evolution of development, behavior, and structure of organisms. The main constraint, over which there has been much debate, is the requirement that each genetic and phenotypic change during evolution should be relatively small, because developmental systems are so complex and interlinked. However, it is not clear what "relatively small" should mean, for example polyploidy in plants is a reasonably common large genetic change (Stebbins, 1950). The origin of eukaryotic endosymbiosis is a more dramatic example (Margulis & Fester, 1991).

All adaptations help organisms survive in their ecological niches. The adaptive traits may be structural, behavioral or physiological. Structural adaptations are physical features of an organism, such as shape, body covering, armament, and internal organization. Behavioral adaptations are inherited systems of behavior, whether inherited in detail as instincts, or as a neuropsychological capacity for learning. Examples include searching for food, mating, and vocalizations. Physiological adaptations permit the organism to perform special functions such as making venom, secreting slime, and phototropism, but also involve more general functions such as growth and development, temperature regulation, ionic balance and other aspects of homeostasis. Adaptation affects all aspects of the life of an organism (Hutchinson, 1965).

The following definitions are given by the evolutionary biologist Theodosius Dobzhansky:

1. *Adaptation* is the evolutionary process whereby an organism becomes better able to live in its habitat or habitats (Dobzhansky, 1968; Wang, 2014; Sejian et al., 2015).

2. *Adaptedness* is the state of being adapted: the degree to which an organism is able to live and reproduce in a given set of habitats (Dobzhansky, 1970).

3. An *adaptive trait* is an aspect of the developmental pattern of the organism which enables or enhances the probability of that organism surviving and reproducing (Dobzhansky, 1956).

What adaptation is not

Adaptation differs from flexibility, acclimatization, and learning, all of which are changes during life which are not inherited. Flexibility deals with the relative capacity of an organism to maintain itself in different habitats: its degree of specialization. Acclimatization describes automatic physiological adjustments during life; learning means improvement in behavioral performance during life (Pillay et al., 2013; Gross, 2012).

Flexibility stems from phenotypic plasticity, the ability of an organism with a given genotype (genetic type) to change its phenotype (observable characteristics) in response to changes in its habitat, or to move to a different habitat (Irwin et al., 2003; Price, 2006). The degree of flexibility is inherited, and varies between individuals. A highly specialized animal or plant lives only in a well-defined habitat, eats a specific type of food, and cannot survive if its needs are not met. Many herbivores are like this; extreme examples are koalas which depend on *Eucalyptus*, and giant pandas which require bamboo. A generalist, on the other hand, eats a range of food, and can survive in many different conditions. Examples are humans, rats, crabs and many carnivores. The *tendency* to behave in a specialized or exploratory manner is inherited—it is an adaptation. Rather different is developmental flexibility: "An animal or plant is developmentally flexible if when it is raised in or transferred to new conditions, it changes in structure so that it is better fitted to survive in the new environment," writes evolutionary biologist John Maynard Smith (Smith, 1993).



Figure 4.1.2**:** Some generalists, such as birds, have the flexibility to adapt to urban areas.

If humans move to a higher altitude, respiration and physical exertion become a problem, but after spending time in high altitude conditions they acclimatize to the reduced partial pressure of oxygen, such as by producing more red blood cells. The ability to acclimatize is an adaptation, but the acclimatization itself is not. The reproductive rate declines, but deaths from some tropical diseases also go down. Over a longer period of time, some people are better able to reproduce at high altitudes than others. They contribute more heavily to later generations, and gradually by natural selection the whole population becomes adapted to the new conditions. This has demonstrably occurred, as the observed performance of long-term communities at higher altitude is significantly better than the performance of new arrivals, even when the new arrivals have had time to acclimatize (Moore & Regensteiner, 1983).

Adaptedness and fitness

There is a relationship between adaptedness and the concept of fitness used in population genetics. Differences in fitness between genotypes predict the rate of evolution by natural selection. Natural selection changes the relative frequencies of alternative phenotypes, insofar as they are heritable (Endler, 1986). However, a phenotype with high adaptedness may not have high fitness. Dobzhansky mentioned the example of the Californian redwood, which is highly adapted, but a relict species in danger of extinction (Dobzhansky, 1968). Elliott Sober commented that adaptation was a retrospective concept since it implied something about the history of a trait, whereas fitness predicts a trait's future (Sober, 1984).

1. Relative fitness- the average contribution to the next generation by a genotype or a class of genotypes, relative to the contributions of other genotypes in the population (Futuyma, 1986). This is also known as *Darwinian fitness*, *selection coefficient*, and other terms.

2. Absolute fitness - the absolute contribution to the next generation by a genotype or a class of genotypes. Also known as the Malthusian parameter when applied to the population as a whole (Endler, 1986; Fisher, 1930).

3. Adaptedness - the extent to which a phenotype fits its local ecological niche. Researchers can sometimes test this through a reciprocal transplant, which involves taking organisms evolved in different locations and swapping where they are located to determine if fitness is reduced. Transplant experiments are often used to test if there is a genetic component to differences in populations (Gaggiotti et al., 2015).

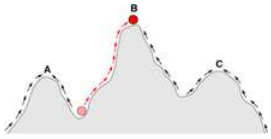


Figure 4.1.3**:** In this sketch of a fitness landscape, a population can evolve by following the arrows to the adaptive peak at point B, and the points A and C are local optima where a population could become trapped.

Sewall Wright proposed that populations occupy *adaptive peaks* on a fitness landscape. To evolve to another, higher peak, a population would first have to pass through a valley of maladaptive intermediate stages, and might be "trapped" on a peak that is not optimally adapted (Wright, 1932).

Definition: Reciprocal transplant experiment

Testing for local adaptation requires measuring the fitness of organisms from one population in both their local environment and in foreign environments. This is often done using transplant experiments. Using the stricter definition of reciprocal home

site advantage, local adaptation is often tested via reciprocal transplant experiments. In reciprocal transplants, organisms from one population are transplanted into another population, and vice versa, and their fitness is measured (see figure) (Ebert & Kawecki, 2004). If local transplants outperform (i.e. have higher fitness than) the foreign transplants at both sites, the local populations are said to be locally adapted (Fenster & Galloway, 2000). If local adaptation is defined simply as a home site advantage of one population (local sources outperform foreign sources at a common site), it can be tested for using common garden experiments, where multiple source populations are grown in a common site, as long as one of the source populations is local to that site.

Transplant experiments have most often been done with plants or other organisms that do not move (Hereford, 2009). However, evidence for rapid local adaptation in mobile animals has been gathered through transplant experiments with Trinidadian guppies (Bryant et al., 2009).

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4.2: Strategies for dealing with a changing environment

There are lots of amazing and sometimes bizarre adaptations out there in the world. For example, some species of frogs (e.g., wood frogs) that live in temperate climates can tolerate the freezing of their blood and other tissues. These frogs allow about 65% of their bodies to freeze solid, stop breathing, and stop their heart when temperatures drop below freezing. Come spring, as temperatures rise, the frog's body thaws and basic motor functions restart, allowing these frogs to survive incredibly harsh winter conditions. Other examples of interesting adaptations include carnivorous plants that obtain their nutrients from insects (e.g., pitcher plants), or rodents (kangaroo rat) that obtain enough water from metabolism that they do not need to drink water at all.



Figure 4.2.1**:** Frog (photo by Patti Black on Unsplash), pitcher plant (photo by Adrian Pingstone released to the public domain), and kangaroo rat (US Fish & Wildlife).

While each of these examples are fascinating in their own right, perhaps a better place to start when thinking about adaptation are the basic, or broad strategies that organisms have adapted to survive in the environment. Specifically, if we think about the fact that the environment that an organism lives in can vary considerably. The environment can vary temporally, on both short and long-term time scales, and spatially in terms of both abiotic and biotic factors. For example, the environment an organism experiences can change in temperature, precipitation, amount of sunlight, water availability, oxygen concentration, salinity, atmospheric pressure, etc. This can create problems for living things because most cellular functions (think enzymes, or neurotransmitters) require specific conditions for proper function. Biotic components of the environment can also change with time or space, including things like the availability of prey, the abundance of predators or competitors, or access to potential mates. While different groups of plants and animals may have solved different components of dealing with this variability in different ways, more broadly we can think of two basic solutions or strategies for dealing with environmental variation: **conform** or **regulate**.

Conforming is when an organism allows their internal environment to fluctuate with the external environment; we might call an organism that conforms a "conformer" for that particular environmental variable. An example of a conformer to external temperature is a frog that allows its body temperature to fluctuate with the environment (Figure 4.2.2A). As the external temperature increases or decreases, the internal temperature of the frog increases or decreases along with the external environment.

If we're thinking just about temperature, we often describe organisms using conforming strategies using the terms **ectotherm** (an animal that relies on the external environment to regulate its internal body temperature), or **poikilotherm** (an animal that varies its internal body temperature within a wide range of temperatures).

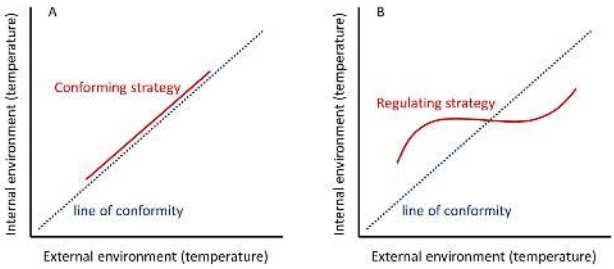


Figure 4.2.2**:** Basic strategies for dealing with fluctuations in the environment: conform or regulate.

Regulating is when an organism attempts to regulate or maintain a constant internal environment despite any environmental fluctuations; we might call an organism that regulates a "regulator" for that particular environmental variable. An example of a regulator for external temperature is a dog that attempts to maintain its internal body temperature within a relatively narrow range despite fluctuations in the external environment (Figure 4.2.2B). As the external temperature increases or decreases, the internal temperature of the dog remains nearly the same with some limitations at extreme temperatures.

If we're thinking just about temperature, we often describe organisms using regulating strategies using the terms **endotherm** (an animal that regulates its own internal body temperature through metabolic processes), or **homeotherm** (maintains a constant internal body temperature, usually within a narrow range of temperatures).

Some organisms can differ in their strategy for different regulatory processes. For example, salmon are **thermoconformers**, but **osmoregulators** when they move between marine (saline) and freshwater environments..

There are costs and benefits to each of these basic strategies. For example, conformers will invest less energy into maintaining their internal environment, but can experience compromised cellular functions. On the other hand, regulators can live in a wider range of environments without experiencing reduced cellular functions, but they expend a great deal of energy to maintain their internal environment (Figure 4.2.3).

	Benefits	Costs
Regulator	Freedom from environment	High energy demand
Conformer	Low energy demand	Compromised homeostasis

Figure 4.2.3**:** Theoretical costs and benefits of an organism regulating their internal environment or conforming to the external environment.

In addition to being a conformer or regulator, organisms may also be **avoiders** that will escape changes in the environment by moving locally or migrating long distances (read more about this in the behavioral ecology chapter). Other types of the "avoiding" strategy could include organisms that undergo some type of **dormancy**, which is when an organism decreases their metabolic activity under extended unfavorable conditions in order to conserve energy.

Examples of dormancy in animals include **hibernation**, a mechanism used by many mammals to reduce energy expenditure and survive food shortages over the winter. During hibernation, the animal undergoes many physiological changes, including decreased heart rate (by as much as 95%) and decreased body temperature. Another type of dormancy in animals, most commonly seen in insects, is **diapause**, when the organism completely suspends development between autumn and spring.

In plants, dormancy is a period of arrested growth, and is a survival strategy exhibited by many plant species that allows them to survive in climates where part of the year is unsuitable for growth, such as winter or dry seasons. A classic example of dormancy in plants is seed dormancy, where seeds are prevented from germinating during unsuitable ecological conditions. Many plant species that exhibit dormancy have a biological clock that tells them when to slow activity and to prepare soft tissues for a period of

freezing temperatures or water shortage. On the other hand, dormancy can be triggered after a normal growing season by decreasing temperatures, shortened day length, and/or a reduction in rainfall.

Many bacteria can survive adverse conditions such as temperature, desiccation, and antibiotics by forming endospores, cysts, or states of reduced metabolic activity lacking specialized cellular structures.

For organisms that regulate components of their internal environment to big changes in the external environment, one key question we might have is: how do they do this? Mechanistically, the process of adjusting the internal environment in response to an external change is described as **acclimation**.

Acclimation

Acclimation is the process in which an individual organism adjusts to a change in its environment (such as a change in altitude, temperature, humidity, photoperiod, or pH), allowing it to maintain fitness across a range of environmental conditions. Acclimation occurs in a short period of time (hours to weeks), and within the organism's lifetime (compared to adaptation, which is evolution, taking place over many generations). This may be a discrete occurrence (for example, when mountaineers acclimate to high altitude over hours or days) or may instead represent part of a periodic cycle, such as a mammal shedding heavy winter fur in favor of a lighter summer coat. Organisms can adjust their morphological, behavioral, physical, and/or biochemical traits in response to changes in their environment (*The Unabridged Hutchinson Encyclopedia*, 2009). While the capacity to acclimate to novel environments has been well documented in thousands of species, researchers still know very little about how and why organisms acclimate the way that they do.

Methods of acclimation

Biochemical

In order to maintain performance across a range of environmental conditions, there are several strategies organisms use to acclimate. In response to changes in temperature, organisms can change the biochemistry of cell membranes making them more fluid in cold temperatures and less fluid in warm temperatures by increasing the number of membrane proteins (Los & Murata, 2004). In response to certain stressors, some organisms express so-called heat shock proteins that act as molecular chaperones and reduce denaturation by guiding the folding and refolding of proteins. It has been shown that organisms which are acclimated to high or low temperatures display relatively high resting levels of heat shock proteins so that when they are exposed to even more extreme temperatures the proteins are readily available. Expression of heat shock proteins and regulation of membrane fluidity are just two of many biochemical methods organisms use to acclimate to novel environments.

Morphological

Organisms are able to change several characteristics relating to their morphology in order to maintain performance in novel environments. For example, birds often increase their organ size to increase their metabolism. This can take the form of an increase in the mass of nutritional organs or heat-producing organs, like the pectorals (with the latter being more consistent across species) (Liknes & Swanson, 2011; McKechnie, 2008).

Examples

Plants

Many plants, such as maple trees, irises, and tomatoes, can survive freezing temperatures if the temperature gradually drops lower and lower each night over a period of days or weeks. The same drop might kill them if it occurred suddenly. Studies have shown that tomato plants that were acclimated to higher temperature over several days were more efficient at photosynthesis at relatively high temperatures than were plants that were not allowed to acclimate (Canejo et al., 2007).

Animals

Animals acclimatize in many ways. Sheep grow very thick wool in cold, damp climates. Fish are able to adjust only gradually to changes in water temperature and quality. Tropical fish sold at pet stores are often kept in acclimation bags until this process is complete. Lowe & Vance (1955) were able to show that lizards acclimated to warm temperatures could maintain a higher running

speed at warmer temperatures than lizards that were not acclimated to warm conditions. Fruit flies that develop at relatively cooler or warmer temperatures have increased cold or heat tolerance as adults, respectively (Slotsbo et al., 2016).

Humans

The salt content of sweat and urine decreases as people acclimatize to hot conditions (U.S. Army, 2007). Plasma volume, heart rate, and capillary activation are also affected (Heat Acclimatization, n.d.).

Acclimation to high altitude continues for months or even years after initial ascent, and ultimately enables humans to survive in an environment that, without acclimation, would kill them. Humans who migrate permanently to a higher altitude naturally acclimatize to their new environment by developing an increase in the number of red blood cells to increase the oxygen carrying capacity of the blood, in order to compensate for lower levels of oxygen intake (Muza et al., 2004; Baillie & Simpson, 2006).

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- Acclimation section from Wikipedia: https://en.wikipedia.org/wiki/Acclimatization
- Information on plant dormancy from: https://en.Wikipedia.org/wiki/Dormancy

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CHAPTER OVERVIEW

Chapter 5: Terrestrial and Aquatic Communities

Learning Objectives

- Objective 1
- Objective 2

5.1: Earth's Biomes

5.1.1: Biogeography

5.1.2: Terrestrial Biomes

5.1.3: Aquatic Biomes

5.1.4: Climate and the Effects of Global Climate Change

Summary

To be added

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5.1: Earth's Biomes

5.01: Earth's Biomes

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5.1.1: Biogeography

Skills to Develop

- Define biogeography
- List and describe abiotic factors that affect the global distribution of plant and animal species
- Compare the impact of abiotic forces on aquatic and terrestrial environments
- Summarize the effect of abiotic factors on net primary productivity

Many forces influence the communities of living organisms present in different parts of the biosphere (all of the parts of Earth inhabited by life). The biosphere extends into the atmosphere (several kilometers above Earth) and into the depths of the oceans. Despite its apparent vastness to an individual human, the biosphere occupies only a minute space when compared to the known universe. Many abiotic forces influence where life can exist and the types of organisms found in different parts of the biosphere. The abiotic factors influence the distribution of biomes: large areas of land with similar climate, flora, and fauna.

Biogeography

Biogeography is the study of the geographic distribution of living things and the abiotic factors that affect their distribution. Abiotic factors such as temperature and rainfall vary based mainly on latitude and elevation. As these abiotic factors change, the composition of plant and animal communities also changes. For example, if you were to begin a journey at the equator and walk north, you would notice gradual changes in plant communities. At the beginning of your journey, you would see tropical wet forests with broad-leaved evergreen trees, which are characteristic of plant communities found near the equator. As you continued to travel north, you would see these broad-leaved evergreen plants eventually give rise to seasonally dry forests with scattered trees. You would also begin to notice changes in temperature and moisture. At about 30 degrees north, these forests would give way to deserts, which are characterized by low precipitation.

Moving farther north, you would see that deserts are replaced by grasslands or prairies. Eventually, grasslands are replaced by deciduous temperate forests. These deciduous forests give way to the boreal forests found in the subarctic, the area south of the Arctic Circle. Finally, you would reach the Arctic tundra, which is found at the most northern latitudes. This trek north reveals gradual changes in both climate and the types of organisms that have adapted to environmental factors associated with ecosystems found at different latitudes. However, different ecosystems exist at the same latitude due in part to abiotic factors such as jet streams, the Gulf Stream, and ocean currents. If you were to hike up a mountain, the changes you would see in the vegetation would parallel those as you move to higher latitudes.

Ecologists who study biogeography examine patterns of species distribution. No species exists everywhere; for example, the Venus flytrap is endemic to a small area in North and South Carolina. An endemic species is one which is naturally found only in a specific geographic area that is usually restricted in size. Other species are generalists: species which live in a wide variety of geographic areas; the raccoon, for example, is native to most of North and Central America.

Species distribution patterns are based on biotic and abiotic factors and their influences during the very long periods of time required for species evolution; therefore, early studies of biogeography were closely linked to the emergence of evolutionary thinking in the eighteenth century. Some of the most distinctive assemblages of plants and animals occur in regions that have been physically separated for millions of years by geographic barriers. Biologists estimate that Australia, for example, has between 600,000 and 700,000 species of plants and animals. Approximately 3/4 of living plant and mammal species are endemic species found solely in Australia (Figure 5.1.1.1).



(a) (b)

Figure \(\PageIndex{1}\): Australia is home to many endemic species. The (a) wallaby (*Wallabia bicolor*), a medium-sized member of the kangaroo family, is a pouched mammal, or marsupial. The (b) echidna (*Tachyglossus aculeatus*) is an egg-laying mammal (credit a: modification of work by Derrick Coetzee; credit b: modification of work by Allan Whittome).

Sometimes ecologists discover unique patterns of species distribution by determining where species are *not* found. Hawaii, for example, has no native land species of reptiles or amphibians, and has only one native terrestrial mammal, the hoary bat. Most of New Guinea, as another example, lacks placental mammals.

Link to Learning

Check out this video to observe a platypus swimming in its natural habitat in New South Wales, Australia.

Plants can be endemic or generalists: endemic plants are found only on specific regions of the Earth, while generalists are found on many regions. Isolated land masses—such as Australia, Hawaii, and Madagascar—often have large numbers of endemic plant species. Some of these plants are endangered due to human activity. The forest gardenia (*Gardenia brighamii*), for instance, is endemic to Hawaii; only an estimated 15–20 trees are thought to exist (Figure 5.1.1.2).



Figure \(\PageIndex{2}\): Listed as federally endangered, the forest gardenia is a small tree with distinctive flowers. It is found only in five of the Hawaiian Islands in small populations consisting of a few individual specimens. *Source: Forest & Kim Starr.*

Energy Sources

Energy from the sun is captured by green plants, algae, cyanobacteria, and photosynthetic protists. These organisms convert solar energy into the chemical energy needed by all living things. Light availability can be an important force directly affecting the evolution of adaptations in photosynthesizers. For instance, plants in the understory of a temperate forest are shaded when the trees above them in the canopy completely leaf out in the late spring. Not surprisingly, understory plants have adaptations to successfully capture available light. One such adaptation is the rapid growth of spring ephemeral plants such as the spring beauty (Figure 5.1.1.3). These spring flowers achieve much of their growth and finish their life cycle (reproduce) early in the season before the trees in the canopy develop leaves.



Figure 5.1.1.3**:** The spring beauty is an ephemeral spring plant that flowers early in the spring to avoid competing with larger forest trees for sunlight. *Source: John Beetham.*

In aquatic ecosystems, the availability of light may be limited because sunlight is absorbed by water, plants (in the water or above the water's surface), suspended particles, and resident microorganisms. Toward the bottom of a lake, pond, or ocean, there is a zone that light cannot reach. Photosynthesis cannot take place there and, as a result, a number of adaptations have evolved that enable living things to survive without light. For instance, aquatic plants have photosynthetic tissue near the surface of the water; for example, think of the broad, floating leaves of a water lily—water lilies cannot survive without light. In environments such as hydrothermal vents, some bacteria extract energy from inorganic chemicals because there is no light for photosynthesis. In small headwater streams in forested areas, very little photosynthesis occurs within the stream because of shading by the forest canopy.

The availability of nutrients in aquatic systems is also an important aspect of energy or photosynthesis. Many organisms sink to the bottom of the ocean when they die in the open water; when this occurs, the energy found in that living organism is sequestered for some time unless ocean upwelling occurs. Ocean upwelling is the rising of deep ocean waters that occurs when prevailing winds blow along surface waters near a coastline (Figure 5.1.1.4). As the wind pushes ocean waters offshore, water from the bottom of the ocean moves up to replace this water. As a result, the nutrients once contained in dead organisms become available for reuse by other living organisms.

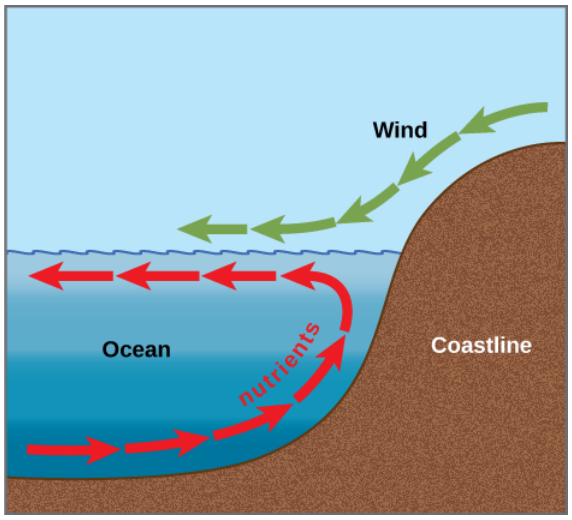


Figure 5.1.1.4**:** Ocean upwelling is an important process that recycles nutrients and energy in the ocean. As wind (green arrows) pushes offshore, it causes water from the ocean bottom (red arrows) to move to the surface, bringing up nutrients from the ocean depths.

In freshwater systems, the recycling of nutrients occurs in response to air temperature changes. The nutrients at the bottom of lakes are recycled twice each year: in the spring and fall turnover. The spring and fall turnover is a seasonal process that recycles nutrients and oxygen from the bottom of a freshwater ecosystem to the top of a body of water (Figure 5.1.1.5). These turnovers are caused by the formation of a thermocline: a layer of water with a temperature that is significantly different from that of the surrounding layers. In wintertime, the surface of lakes found in many northern regions is frozen. However, the water under the ice is slightly warmer, and the water at the bottom of the lake is warmer yet at 4 °C to 5 °C (39.2 °F to 41 °F). Water is densest at 4 °C; therefore, the deepest water is also the densest. The deepest water is oxygen poor because the decomposition of organic material at the bottom of the lake uses up available oxygen that cannot be replaced by means of oxygen diffusion into the water due to the surface ice layer.

Art Connection

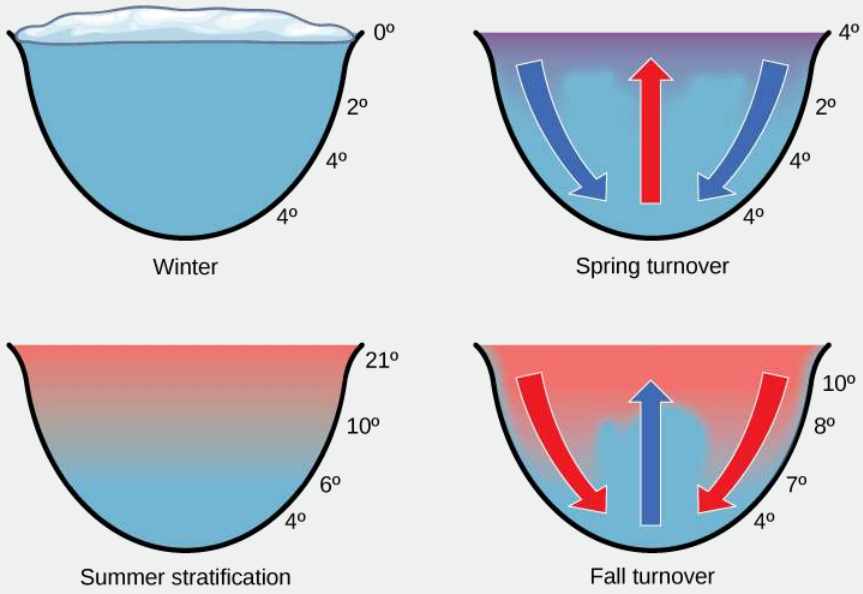


Figure 5.1.1.5**:**
The spring and fall turnovers are important processes in freshwater lakes that act to move the nutrients and oxygen at the bottom of deep lakes to the top. Turnover occurs because water has a maximum density at 4 °C. Surface water temperature changes as the seasons progress, and denser water sinks.

Exercise 5.1.1.1

How might turnover in tropical lakes differ from turnover in lakes that exist in temperate regions?

Answer

Tropical lakes don't freeze, so they don't undergo spring turnover in the same way temperate lakes do. However, stratification does occur, as well as seasonal turnover.

In springtime, air temperatures increase and surface ice melts. When the temperature of the surface water begins to reach 4 °C, the water becomes heavier and sinks to the bottom. The water at the bottom of the lake is then displaced by the heavier surface water and, thus, rises to the top. As that water rises to the top, the sediments and nutrients from the lake bottom are brought along with it. During the summer months, the lake water stratifies, or forms layers, with the warmest water at the lake surface.

As air temperatures drop in the fall, the temperature of the lake water cools to 4 °C; therefore, this causes fall turnover as the heavy cold water sinks and displaces the water at the bottom. The oxygen-rich water at the surface of the lake then moves to the bottom of the lake, while the nutrients at the bottom of the lake rise to the surface (Figure 5.1.1.5). During the winter, the oxygen at the bottom of the lake is used by decomposers and other organisms requiring oxygen, such as fish.

Temperature

Temperature affects the physiology of living things as well as the density and state of water. Temperature exerts an important influence on living things because few living things can survive at temperatures below 0 °C (32 °F) due to metabolic constraints. It is also rare for living things to survive at temperatures exceeding 45 °C (113 °F); this is a reflection of evolutionary response to typical temperatures. Enzymes are most efficient within a narrow and specific range of temperatures; enzyme degradation can occur at higher temperatures. Therefore, organisms either must maintain an internal temperature or they must inhabit an environment that will keep the body within a temperature range that supports metabolism. Some animals have adapted to enable their bodies to survive significant temperature fluctuations, such as seen in hibernation or reptilian torpor. Similarly, some bacteria

are adapted to surviving in extremely hot temperatures such as geysers. Such bacteria are examples of extremophiles: organisms that thrive in extreme environments.

Temperature can limit the distribution of living things. Animals faced with temperature fluctuations may respond with adaptations, such as migration, in order to survive. Migration, the movement from one place to another, is an adaptation found in many animals, including many that inhabit seasonally cold climates. Migration solves problems related to temperature, locating food, and finding a mate. In migration, for instance, the Arctic Tern (*Sterna paradisaea*) makes a 40,000 km (24,000 mi) round trip flight each year between its feeding grounds in the southern hemisphere and its breeding grounds in the Arctic Ocean. Monarch butterflies (*Danaus plexippus*) live in the eastern United States in the warmer months and migrate to Mexico and the southern United States in the wintertime. Some species of mammals also make migratory forays. Reindeer (*Rangifer tarandus*) travel about 5,000 km (3,100 mi) each year to find food. Amphibians and reptiles are more limited in their distribution because they lack migratory ability. Not all animals that can migrate do so: migration carries risk and comes at a high energy cost.

Some animals hibernate or estivate to survive hostile temperatures. Hibernation enables animals to survive cold conditions, and estivation allows animals to survive the hostile conditions of a hot, dry climate. Animals that hibernate or estivate enter a state known as torpor: a condition in which their metabolic rate is significantly lowered. This enables the animal to wait until its environment better supports its survival. Some amphibians, such as the wood frog (*Rana sylvatica*), have an antifreeze-like chemical in their cells, which retains the cells' integrity and prevents them from bursting.

Water

Water is required by all living things because it is critical for cellular processes. Since terrestrial organisms lose water to the environment by simple diffusion, they have evolved many adaptations to retain water.

- Plants have a number of interesting features on their leaves, such as leaf hairs and a waxy cuticle, that serve to decrease the rate of water loss via transpiration.
- Freshwater organisms are surrounded by water and are constantly in danger of having water rush into their cells because of osmosis. Many adaptations of organisms living in freshwater environments have evolved to ensure that solute concentrations in their bodies remain within appropriate levels. One such adaptation is the excretion of dilute urine.
- Marine organisms are surrounded by water with a higher solute concentration than the organism and, thus, are in danger of losing water to the environment because of osmosis. These organisms have morphological and physiological adaptations to retain water and release solutes into the environment. For example, Marine iguanas (*Amblyrhynchus cristatus*), sneeze out water vapor that is high in salt in order to maintain solute concentrations within an acceptable range while swimming in the ocean and eating marine plants.

Inorganic Nutrients and Soil

Inorganic nutrients, such as nitrogen and phosphorus, are important in the distribution and the abundance of living things. Plants obtain these inorganic nutrients from the soil when water moves into the plant through the roots. Therefore, soil structure (particle size of soil components), soil pH, and soil nutrient content play an important role in the distribution of plants. Animals obtain inorganic nutrients from the food they consume. Therefore, animal distributions are related to the distribution of what they eat. In some cases, animals will follow their food resource as it moves through the environment.

Other Aquatic Factors

Some abiotic factors, such as oxygen, are important in aquatic ecosystems as well as terrestrial environments. Terrestrial animals obtain oxygen from the air they breathe. Oxygen availability can be an issue for organisms living at very high elevations, however, where there are fewer molecules of oxygen in the air. In aquatic systems, the concentration of dissolved oxygen is related to water temperature and the speed at which the water moves. Cold water has more dissolved oxygen than warmer water. In addition, salinity, current, and tide can be important abiotic factors in aquatic ecosystems.

Other Terrestrial Factors

Wind can be an important abiotic factor because it influences the rate of evaporation and transpiration. The physical force of wind is also important because it can move soil, water, or other abiotic factors, as well as an ecosystem's organisms.

Fire is another terrestrial factor that can be an important agent of disturbance in terrestrial ecosystems. Some organisms are adapted to fire and, thus, require the high heat associated with fire to complete a part of their life cycle. For example, the jack pine—a coniferous tree—requires heat from fire for its seed cones to open (Figure 5.1.1.6). Through the burning of pine needles, fire adds nitrogen to the soil and limits competition by destroying undergrowth.



Figure 5.1.1.6**:** The mature cones of the jack pine (*Pinus banksiana*) open only when exposed to high temperatures, such as during a forest fire. A fire is likely to kill most vegetation, so a seedling that germinates after a fire is more likely to receive ample sunlight than one that germinates under normal conditions. *Source: USDA.*

Abiotic Factors Influencing Plant Growth

Temperature and moisture are important influences on plant production (primary productivity) and the amount of organic matter available as food (net primary productivity). Net primary productivity is an estimation of all of the organic matter available as food; it is calculated as the total amount of carbon fixed per year minus the amount that is oxidized during cellular respiration. In terrestrial environments, net primary productivity is estimated by measuring the aboveground biomass per unit area, which is the total mass of living plants, excluding roots. This means that a large percentage of plant biomass which exists underground is not included in this measurement. Net primary productivity is an important variable when considering differences in biomes. Very productive biomes have a high level of aboveground biomass.

Annual biomass production is directly related to the abiotic components of the environment. Environments with the greatest amount of biomass have conditions in which photosynthesis, plant growth, and the resulting net primary productivity are optimized. The climate of these areas is warm and wet. Photosynthesis can proceed at a high rate, enzymes can work most efficiently, and stomata can remain open without the risk of excessive transpiration; together, these factors lead to the maximal amount of carbon dioxide (CO_2) moving into the plant, resulting in high biomass production. The aboveground biomass produces several important resources for other living things, including habitat and food. Conversely, dry and cold environments have lower photosynthetic rates and therefore less biomass. The animal communities living there will also be affected by the decrease in available food.

Summary

Biogeography is the study of the geographic distribution of living things and the abiotic factors that affect their distribution. Endemic species are species that are naturally found only in a specific geographic area. The distribution of living things is influenced by several environmental factors that are, in part, controlled by the latitude or elevation at which an organism is found. Ocean upwelling and spring and fall turnovers are important processes regulating the distribution of nutrients and other abiotic factors important in aquatic ecosystems. Energy sources, temperature, water, inorganic nutrients, and soil are factors limiting the distribution of living things in terrestrial systems. Net primary productivity is a measure of the amount of biomass produced by a biome.

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5.1.2: Terrestrial Biomes

The Earth's biomes are categorized into two major groups: terrestrial and aquatic. Terrestrial biomes are based on land, while aquatic biomes include both ocean and freshwater biomes. The eight major terrestrial biomes on Earth are each distinguished by characteristic temperatures and amount of precipitation. Comparing the annual totals of precipitation and fluctuations in precipitation from one biome to another provides clues as to the importance of abiotic factors in the distribution of biomes. Temperature variation on a daily and seasonal basis is also important for predicting the geographic distribution of the biome and the vegetation type in the biome. The distribution of these biomes shows that the same biome can occur in geographically distinct areas with similar climates (Figure 5.1.2.1).

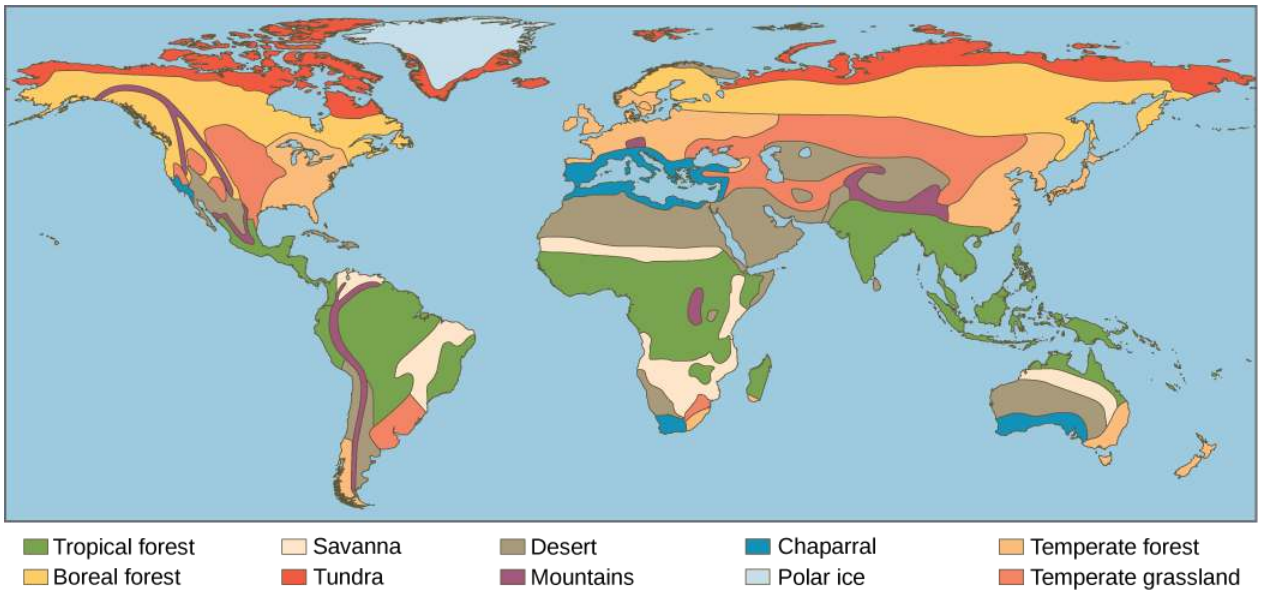


Figure 5.1.2.1: Each of the world's major biomes is distinguished by characteristic temperatures and amounts of precipitation. Polar ice and mountains are also shown.

Tropical Wet Forest

Tropical wet forests are also referred to as tropical rainforests. This biome is found in equatorial regions (Figure 5.1.2.1). The vegetation is characterized by plants with broad leaves that fall off throughout the year. Unlike the trees of deciduous forests, the trees in this biome do not have a seasonal loss of leaves associated with variations in temperature and sunlight; these forests are "evergreen" year-round.

The temperature and sunlight profiles of tropical wet forests are very stable in comparison to that of other terrestrial biomes, with the temperatures ranging from 20 °C to 34 °C (68 °F to 93 °F). When one compares the annual temperature variation of tropical wet forests with that of other forest biomes, the lack of seasonal temperature variation in the tropical wet forest becomes apparent. This lack of seasonality leads to year-round plant growth, rather than the seasonal (spring, summer, and fall) growth seen in other biomes. In contrast to other ecosystems, tropical ecosystems do not have long days and short days during the yearly cycle. Instead, a constant daily amount of sunlight (11–12 hrs per day) provides more solar radiation, thereby, a longer period of time for plant growth.

The annual rainfall in tropical wet forests ranges from 125 to 660 cm (50–200 in) with some monthly variation. While sunlight and temperature remain fairly consistent, annual rainfall is highly variable. Tropical wet forests have wet months in which there can be more than 30 cm (11–12 in) of precipitation, as well as dry months in which there are fewer than 10 cm (3.5 in) of rainfall. However, the driest month of a tropical wet forest still exceeds the *annual* rainfall of some other biomes, such as deserts.

Tropical wet forests have high net primary productivity because the annual temperatures and precipitation values in these areas are ideal for plant growth. Therefore, the extensive biomass present in the tropical wet forest leads to plant communities with very high

species diversities (Figure 5.1.2.2). Tropical wet forests have more species of trees than any other biome; on average between 100 and 300 species of trees are present in a single hectare (2.5 acres) of South America. One way to visualize this is to compare the distinctive horizontal layers within the tropical wet forest biome. On the forest floor is a sparse layer of plants and decaying plant matter. Above that is an understory of short shrubby foliage. A layer of trees rises above this understory and is topped by a closed upper canopy—the uppermost overhead layer of branches and leaves. Some additional trees emerge through this closed upper canopy. These layers provide diverse and complex habitats for the variety of plants, fungi, animals, and other organisms within the tropical wet forests. For instance, epiphytes are plants that grow on other plants, which typically are not harmed. Epiphytes are found throughout tropical wet forest biomes. Many species of animals use the variety of plants and the complex structure of the tropical wet forests for food and shelter. Some organisms live several meters above ground and have adapted to this arboreal lifestyle.



Figure 5.1.2.2: Tropical wet forests, such as these forests of Madre de Dios, Peru, near the Amazon River, have high species diversity. *Source: Roosevelt Garcia.*

Savannas

Savannas are grasslands with scattered trees, and they are located in Africa, South America, and northern Australia (Figure 5.1.2.3). Savannas are hot, tropical areas with temperatures averaging from 24 °C to 29 °C (75 °F to 84 °F) and an annual rainfall of 10–40 cm (3.9–15.7 in). Savannas have an extensive dry season; for this reason, forest trees do not grow as well as they do in the tropical wet forest (or other forest biomes). As a result, within the grasses and forbs (herbaceous flowering plants) that dominate the savanna, there are relatively few trees (Figure 5.1.2.3). Since fire is an important source of disturbance in this biome, plants have evolved well-developed root systems that allow them to quickly re-sprout after a fire.



Figure 5.1.2.3: Savannas, like this one in Taita Hills Wildlife Sanctuary in Kenya, are dominated by grasses. *Source: Christopher T. Cooper.*

Subtropical Deserts

Subtropical deserts exist between 15 ° and 30 ° north and south latitude and are centered on the Tropics of Cancer and Capricorn (Figure 5.1.2.4). This biome is very dry; in some years, evaporation exceeds precipitation. Subtropical hot deserts can have daytime soil surface temperatures above 60 °C (140 °F) and nighttime temperatures approaching 0 °C (32 °F). In cold deserts, temperatures can be as high as 25 °C and can drop below -30 °C (-22 °F). Subtropical deserts are characterized by low annual precipitation of fewer than 30 cm (12 in) with little monthly variation and lack of predictability in rainfall. In some cases, the annual rainfall can be as low as 2 cm (0.8 in) in subtropical deserts located in central Australia (“the Outback”) and northern Africa.

The vegetation and low animal diversity of this biome is closely related to this low and unpredictable precipitation. Very dry deserts lack perennial vegetation that lives from one year to the next; instead, many plants are annuals that grow quickly and reproduce when rainfall does occur, then they die. Many other plants in these areas are characterized by having a number of adaptations that conserve water, such as deep roots, reduced foliage, and water-storing stems (Figure 5.1.2.4). Seed plants in the desert produce seeds that can be in dormancy for extended periods between rains. Adaptations in desert animals include nocturnal behavior and burrowing.



Figure 5.1.2.4: To reduce water loss, many desert plants have tiny leaves or no leaves at all. The leaves of ocotillo (*Fouquieria splendens*), shown here in the Sonora Desert near Gila Bend, Arizona, appear only after rainfall, and then are shed.

Chaparral

The chaparral is also called the scrub forest and is found in California, along the Mediterranean Sea, and along the southern coast of Australia (Figure 5.1.2.5). The annual rainfall in this biome ranges from 65 cm to 75 cm (25.6–29.5 in), and the majority of the rain falls in the winter. Summers are very dry and many chaparral plants are dormant during the summertime. The chaparral vegetation, shown in Figure 5.1.2.5, is dominated by shrubs and is adapted to periodic fires, with some plants producing seeds that only germinate after a hot fire. The ashes left behind after a fire are rich in nutrients like nitrogen that fertilize the soil and promote plant regrowth.



Figure 5.1.2.5: The chaparral is dominated by shrubs. *Source: Miguel Vieira.*

Temperate Grasslands

Temperate grasslands are found throughout central North America, where they are also known as prairies; they are also in Eurasia, where they are known as steppes (Figure 5.1.2.6). Temperate grasslands have pronounced annual fluctuations in temperature with hot summers and cold winters. The annual temperature variation produces specific growing seasons for plants. Plant growth is possible when temperatures are warm enough to sustain plant growth and when ample water is available, which occurs in the spring, summer, and fall. During much of the winter, temperatures are low, and water, which is stored in the form of ice, is not available for plant growth.

Annual precipitation ranges from 25 cm to 75 cm (9.8–29.5 in). Because of relatively lower annual precipitation in temperate grasslands, there are few trees except for those found growing along rivers or streams. The dominant vegetation tends to consist of grasses and some prairies sustain populations of grazing animals Figure 5.1.2.6. The vegetation is very dense and the soils are fertile because the subsurface of the soil is packed with the roots and rhizomes (underground stems) of these grasses. The roots and rhizomes act to anchor plants into the ground and replenish the organic material (humus) in the soil when they die and decay.



Figure 5.1.2.6: The American bison (*Bison bison*), more commonly called the buffalo, is a grazing mammal that once populated American prairies in huge numbers. *Source: Jack Dykinga, USDA Agricultural Research Service.*

Fires, mainly caused by lightning, are a natural disturbance in temperate grasslands. When fire is suppressed in temperate grasslands, the vegetation eventually converts to scrub and dense forests. Often, the restoration or management of temperate grasslands requires the use of controlled burns to suppress the growth of trees and maintain the grasses.

Temperate Forests

Temperate forests are the most common biome in eastern North America, Western Europe, Eastern Asia, Chile, and New Zealand (Figure 5.1.2.7). This biome is found throughout mid-latitude regions. Temperatures range between -30 °C and 30 °C (-22 °F to 86 °F) and drop to below freezing on an annual basis. These temperatures mean that temperate forests have defined growing seasons during the spring, summer, and early fall. Precipitation is relatively constant throughout the year and ranges between 75 cm and 150 cm (29.5–59 in).

Because of the moderate annual rainfall and temperatures, deciduous trees are the dominant plant in this biome (Figure 5.1.2.7). Deciduous trees lose their leaves each fall and remain leafless in the winter. Thus, no photosynthesis occurs in the deciduous trees during the dormant winter period. Each spring, new leaves appear as the temperature increases. Because of the dormant period, the net primary productivity of temperate forests is less than that of tropical wet forests. In addition, temperate forests show less diversity of tree species than tropical wet forest biomes.



Figure 5.1.2.7: Deciduous trees are the dominant plant in the temperate forest. *Source: Oliver Herold.*

The trees of the temperate forests leaf out and shade much of the ground; however, this biome is more open than tropical wet forests because trees in the temperate forests do not grow as tall as the trees in tropical wet forests. The soils of the temperate forests are rich in inorganic and organic nutrients. This is due to the thick layer of leaf litter on forest floors. As this leaf litter decays, nutrients are returned to the soil. The leaf litter also protects soil from erosion, insulates the ground, and provides habitats for invertebrates (such as the pill bug or roly-poly, *Armadillidium vulgare*) and their predators, such as the red-backed salamander (*Plethodon cinereus*).

Boreal Forests

The boreal forest, also known as taiga or coniferous forest, is found south of the Arctic Circle and across most of Canada, Alaska, Russia, and northern Europe (Figure 5.1.2.8). This biome has cold, dry winters and short, cool, wet summers. The annual precipitation is from 40 cm to 100 cm (15.7–39 in) and usually takes the form of snow. Little evaporation occurs because of the cold temperatures.

The long and cold winters in the boreal forest have led to the predominance of cold-tolerant cone-bearing plants. These are evergreen coniferous trees like pines, spruce, and fir, which retain their needle-shaped leaves year-round. Evergreen trees can photosynthesize earlier in the spring than deciduous trees because less energy from the sun is required to warm a needle-like leaf than a broad leaf. This benefits evergreen trees, which grow faster than deciduous trees in the boreal forest. In addition, soils in boreal forest regions tend to be acidic with little available nitrogen. Leaves are a nitrogen-rich structure and deciduous trees must produce a new set of these nitrogen-rich structures each year. Therefore, coniferous trees that retain nitrogen-rich needles may have a competitive advantage over the broad-leafed deciduous trees.

The net primary productivity of boreal forests is lower than that of temperate forests and tropical wet forests. The aboveground biomass of boreal forests is high because these slow-growing tree species are long lived and accumulate standing biomass over time. Plant species diversity is less than that seen in temperate forests and tropical wet forests. Boreal forests lack the pronounced elements of the layered forest structure seen in tropical wet forests. The structure of a boreal forest is often only a tree layer and a ground layer (Figure 5.1.2.8). When conifer needles are dropped, they decompose more slowly than broad leaves; therefore, fewer nutrients are returned to the soil to fuel plant growth.



Figure 5.1.2.8: The boreal forest (taiga) has low lying plants and conifer trees. *Source: L.B. Brubaker.*

Arctic Tundra

The Arctic tundra lies north of the subarctic boreal forest and is located throughout the Arctic regions of the northern hemisphere (Figure 5.1.2.9). The average winter temperature is -34 °C (-34 °F) and the average summer temperature is from 3 °C to 12 °C (37 °F–52 °F). Plants in the arctic tundra have a very short growing season of approximately 10–12 weeks. However, during this time, there are almost 24 hours of daylight and plant growth is rapid. The annual precipitation of the Arctic tundra is very low with little annual variation in precipitation. And, as in the boreal forests, there is little evaporation due to the cold temperatures.

Plants in the Arctic tundra are generally low to the ground (Figure 5.1.2.9). There is little species diversity, low net primary productivity, and low aboveground biomass. The soils of the Arctic tundra may remain in a perennially frozen state referred to as permafrost. The permafrost makes it impossible for roots to penetrate deep into the soil and slows the decay of organic matter, which inhibits the release of nutrients from organic matter. During the growing season, the ground of the Arctic tundra can be completely covered with plants or lichens.



Figure 5.1.2.9: Low-growing plants such as shrub willow dominate the tundra landscape, shown here in the Arctic National Wildlife Refuge. *Source: USFWS Arctic National Wildlife Refuge.*

Link to Learning



Watch this *Assignment Discovery: Biomes* video for an overview of biomes. To explore further, select one of the biomes on the extended playlist: desert, savanna, temperate forest, temperate grassland, tropic, tundra.

Summary

The Earth has terrestrial biomes and aquatic biomes. Aquatic biomes include both freshwater and marine environments. There are eight major terrestrial biomes: tropical wet forests, savannas, subtropical deserts, chaparral, temperate grasslands, temperate forests, boreal forests, and Arctic tundra. The same biome can occur in different geographic locations with similar climates. Temperature and precipitation, and variations in both, are key abiotic factors that shape the composition of animal and plant communities in terrestrial biomes. Some biomes, such as temperate grasslands and temperate forests, have distinct seasons, with cold weather and hot weather alternating throughout the year. In warm, moist biomes, such as the tropical wet forest, net primary productivity is high, as warm temperatures, abundant water, and a year-round growing season fuel plant growth. Other biomes, such as deserts and tundra, have low primary productivity due to extreme temperatures and a shortage of available water.

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5.1.3: Aquatic Biomes

Abiotic Factors Influencing Aquatic Biomes

Like terrestrial biomes, aquatic biomes are influenced by a series of abiotic factors. The aquatic medium—water— has different physical and chemical properties than air, however. Even if the water in a pond or other body of water is perfectly clear (there are no suspended particles), water, on its own, absorbs light. As one descends into a deep body of water, there will eventually be a depth which the sunlight cannot reach. While there are some abiotic and biotic factors in a terrestrial ecosystem that might obscure light (like fog, dust, or insect swarms), usually these are not permanent features of the environment. The importance of light in aquatic biomes is central to the communities of organisms found in both freshwater and marine ecosystems. In freshwater systems, stratification due to differences in density is perhaps the most critical abiotic factor and is related to the energy aspects of light. The thermal properties of water (rates of heating and cooling) are significant to the function of marine systems and have major impacts on global climate and weather patterns. Marine systems are also influenced by large-scale physical water movements, such as currents; these are less important in most freshwater lakes.

The ocean is categorized by several areas or zones (Figure 5.1.3.1). All of the ocean's open water is referred to as the pelagic realm (or zone). The benthic realm (or zone) extends along the ocean bottom from the shoreline to the deepest parts of the ocean floor. Within the pelagic realm is the photic zone, which is the portion of the ocean that light can penetrate (approximately 200 m or 650 ft). At depths greater than 200 m, light cannot penetrate; thus, this is referred to as the aphotic zone. The majority of the ocean is aphotic and lacks sufficient light for photosynthesis. The deepest part of the ocean, the Challenger Deep (in the Mariana Trench, located in the western Pacific Ocean), is about 11,000 m (about 6.8 mi) deep. To give some perspective on the depth of this trench, the ocean is, on average, 4267 m or 14,000 ft deep. These realms and zones are relevant to freshwater lakes as well.

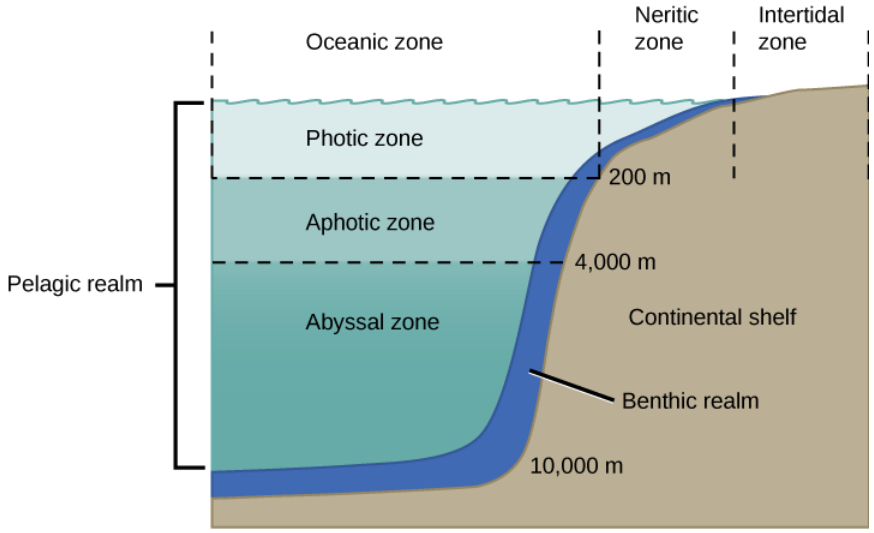


Figure 5.1.3.1: The ocean is divided into different zones based on water depth and distance from the shoreline.

Marine Biomes

The ocean is the largest marine biome. It is a continuous body of salt water that is relatively uniform in chemical composition; it is a weak solution of mineral salts and decayed biological matter. Within the ocean, coral reefs are a second kind of marine biome. Estuaries, coastal areas where salt water and fresh water mix, form a third unique marine biome.

Ocean

The physical diversity of the ocean is a significant influence on plants, animals, and other organisms. The ocean is categorized into different zones based on how far light reaches into the water. Each zone has a distinct group of species adapted to the biotic and abiotic conditions particular to that zone.

The intertidal zone, which is the zone between high and low tide, is the oceanic region that is closest to land (Figure 5.1.3.1). Generally, most people think of this portion of the ocean as a sandy beach. In some cases, the intertidal zone is indeed a sandy

beach, but it can also be rocky or muddy. The intertidal zone is an extremely variable environment because of tides. Organisms are exposed to air and sunlight at low tide and are underwater most of the time, especially during high tide. Therefore, living things that thrive in the intertidal zone are adapted to being dry for long periods of time. The shore of the intertidal zone is also repeatedly struck by waves, and the organisms found there are adapted to withstand damage from the pounding action of the waves (Figure 5.1.3.2). The exoskeletons of shoreline crustaceans (such as the shore crab, *Carcinus maenas*) are tough and protect them from desiccation (drying out) and wave damage. Another consequence of the pounding waves is that few algae and plants establish themselves in the constantly moving rocks, sand, or mud.



Figure 5.1.3.2: Sea urchins, mussel shells, and starfish are often found in the intertidal zone, shown here in Kachemak Bay, Alaska. *Source: NOAA.*

The neritic zone (Figure 5.1.3.1) extends from the intertidal zone to depths of about 200 m (or 650 ft) at the edge of the continental shelf. Since light can penetrate this depth, photosynthesis can occur in the neritic zone. The water here contains silt and is well-oxygenated, low in pressure, and stable in temperature. Phytoplankton and floating *Sargassum* (a type of free-floating marine seaweed) provide a habitat for some sea life found in the neritic zone. Zooplankton, protists, small fishes, and shrimp are found in the neritic zone and are the base of the food chain for most of the world's fisheries.

Beyond the neritic zone is the open ocean area known as the oceanic zone (Figure 5.1.3.1). Within the oceanic zone there is thermal stratification where warm and cold waters mix because of ocean currents. Abundant plankton serve as the base of the food chain for larger animals such as whales and dolphins. Nutrients are scarce and this is a relatively less productive part of the marine biome. When photosynthetic organisms and the protists and animals that feed on them die, their bodies fall to the bottom of the ocean where they remain; unlike freshwater lakes, the open ocean lacks a process for bringing the organic nutrients back up to the surface. The majority of organisms in the aphotic zone include sea cucumbers (*phylum Echinodermata*) and other organisms that survive on the nutrients contained in the dead bodies of organisms in the photic zone.

Beneath the pelagic zone is the benthic realm, the deepwater region beyond the continental shelf (Figure 5.1.3.1). The bottom of the benthic realm is comprised of sand, silt, and dead organisms. Temperature decreases, remaining above freezing, as water depth increases. This is a nutrient-rich portion of the ocean because of the dead organisms that fall from the upper layers of the ocean. Because of this high level of nutrients, a diversity of fungi, sponges, sea anemones, marine worms, sea stars, fishes, and bacteria exist.

The deepest part of the ocean is the abyssal zone, which is at depths of 4000 m or greater. The abyssal zone (Figure 5.1.3.1) is very cold and has very high pressure, high oxygen content, and low nutrient content. There are a variety of invertebrates and fishes found in this zone, but the abyssal zone does not have plants because of the lack of light. Hydrothermal vents are found primarily in the abyssal zone; chemosynthetic bacteria utilize the hydrogen sulfide and other minerals emitted from the vents. These chemosynthetic bacteria use the hydrogen sulfide as an energy source and serve as the base of the food chain found in the abyssal zone.

Coral Reefs

Coral reefs are ocean ridges formed by marine invertebrates living in warm shallow waters within the photic zone of the ocean. They are found within 30˚ north and south of the equator. The Great Barrier Reef is a well-known reef system located several miles off the northeastern coast of Australia. Other coral reef systems are fringing islands, which are directly adjacent to land, or atolls, which are circular reef systems surrounding a former landmass that is now underwater. The coral organisms (members of phylum Cnidaria) are colonies of saltwater polyps that secrete a calcium carbonate skeleton. These calcium-rich skeletons slowly accumulate, forming the underwater reef (Figure 5.1.3.3). Corals found in shallower waters (at a depth of approximately 60 m or about 200 ft) have a mutualistic relationship with photosynthetic unicellular algae. The relationship provides corals with the majority of the nutrition and the energy they require. The waters in which these corals live are nutritionally poor and, without this mutualism, it would not be possible for large corals to grow. Some corals living in deeper and colder water do not have a mutualistic relationship with algae; these corals attain energy and nutrients using stinging cells on their tentacles to capture prey.

It is estimated that more than 4,000 fish species inhabit coral reefs. These fishes can feed on coral, the cryptofauna (invertebrates found within the calcium carbonate substrate of the coral reefs), or the seaweed and algae that are associated with the coral. In addition, some fish species inhabit the boundaries of a coral reef; these species include predators, herbivores, or planktivores. Predators are animal species that hunt and are carnivores or “flesh eaters.” Herbivores eat plant material, and planktivores eat plankton.



Figure 5.1.3.3: Coral reefs are formed by the calcium carbonate skeletons of coral organisms, which are marine invertebrates in the phylum Cnidaria. *Source: Terry Hughes.*

Evolution Connection: Global Decline of Coral Reefs

It takes a long time to build a coral reef. The animals that create coral reefs have evolved over millions of years, continuing to slowly deposit the calcium carbonate that forms their characteristic ocean homes. Bathed in warm tropical waters, the coral animals and their symbiotic algal partners evolved to survive at the upper limit of ocean water temperature.

Together, climate change and human activity pose dual threats to the long-term survival of the world's coral reefs. As global warming due to fossil fuel emissions raises ocean temperatures, coral reefs are suffering. The excessive warmth causes the reefs to expel their symbiotic, food-producing algae, resulting in a phenomenon known as bleaching. When bleaching occurs, the reefs lose much of their characteristic color as the algae and the coral animals die if loss of the symbiotic zooxanthellae is prolonged.

Rising levels of atmospheric carbon dioxide further threaten the corals in other ways; as CO_2 dissolves in ocean waters, it lowers the pH and increases ocean acidity. As acidity increases, it interferes with the calcification that normally occurs as coral animals build their calcium carbonate homes.

When a coral reef begins to die, species diversity plummets as animals lose food and shelter. Coral reefs are also economically important tourist destinations, so the decline of coral reefs poses a serious threat to coastal economies.

Human population growth has damaged corals in other ways, too. As human coastal populations increase, the runoff of sediment and agricultural chemicals has increased, too, causing some of the once-clear tropical waters to become cloudy. At the same time, overfishing of popular fish species has allowed the predator species that eat corals to go unchecked.

Although a rise in global temperatures of 1–2˚C (a conservative scientific projection) in the coming decades may not seem large, it is very significant to this biome. When change occurs rapidly, species can become extinct before evolution leads to new adaptations. Many scientists believe that global warming, with its rapid (in terms of evolutionary time) and inexorable increases in temperature, is tipping the balance beyond the point at which many of the world's coral reefs can recover.

Estuaries: Where the Ocean Meets Fresh Water

Estuaries are biomes that occur where a source of fresh water, such as a river, meets the ocean. Therefore, both fresh water and salt water are found in the same vicinity; mixing results in a diluted (brackish) saltwater. Estuaries form protected areas where many of the young offspring of crustaceans, mollusks, and fish begin their lives. Salinity is a very important factor that influences the organisms and the adaptations of the organisms found in estuaries. The salinity of estuaries varies and is based on the rate of flow of its freshwater sources. Once or twice a day, high tides bring salt water into the estuary. Low tides occurring at the same frequency reverse the current of salt water.

The short-term and rapid variation in salinity due to the mixing of fresh water and salt water is a difficult physiological challenge for the plants and animals that inhabit estuaries. Many estuarine plant species are halophytes: plants that can tolerate salty conditions. Halophytic plants are adapted to deal with the salinity resulting from saltwater on their roots or from sea spray. In some halophytes, filters in the roots remove the salt from the water that the plant absorbs. Other plants are able to pump oxygen into their roots. Animals, such as mussels and clams (*phylum Mollusca*), have developed behavioral adaptations that expend a lot of energy to function in this rapidly changing environment. When these animals are exposed to low salinity, they stop feeding, close their shells, and switch from aerobic respiration (in which they use gills) to anaerobic respiration (a process that does not require oxygen). When high tide returns to the estuary, the salinity and oxygen content of the water increases, and these animals open their shells, begin feeding, and return to aerobic respiration.

Freshwater Biomes

Freshwater biomes include lakes and ponds (standing water) as well as rivers and streams (flowing water). They also include wetlands, which will be discussed later. Humans rely on freshwater biomes to provide aquatic resources for drinking water, crop irrigation, sanitation, and industry. These various roles and human benefits are referred to as ecosystem services. Lakes and ponds are found in terrestrial landscapes and are, therefore, connected with abiotic and biotic factors influencing these terrestrial biomes.

Lakes and Ponds

Lakes and ponds can range in area from a few square meters to thousands of square kilometers. Temperature is an important abiotic factor affecting living things found in lakes and ponds. In the summer, thermal stratification of lakes and ponds occurs when the upper layer of water is warmed by the sun and does not mix with deeper, cooler water. Light can penetrate within the photic zone of the lake or pond. Phytoplankton (algae and cyanobacteria) are found here and carry out photosynthesis, providing the base of the food web of lakes and ponds. Zooplankton, such as rotifers and small crustaceans, consume these phytoplankton. At the bottom of lakes and ponds, bacteria in the aphotic zone break down dead organisms that sink to the bottom.

Nitrogen and phosphorus are important limiting nutrients in lakes and ponds. Because of this, they are determining factors in the amount of phytoplankton growth in lakes and ponds. When there is a large input of nitrogen and phosphorus (from sewage and runoff from fertilized lawns and farms, for example), the growth of algae skyrockets, resulting in a large accumulation of algae called an algal bloom. Algal blooms (Figure 5.1.3.4) can become so extensive that they reduce light penetration in water. As a result, the lake or pond becomes aphotic and photosynthetic plants cannot survive. When the algae die and decompose, severe oxygen depletion of the water occurs. Fishes and other organisms that require oxygen are then more likely to die, and resulting dead zones are found across the globe. Lake Erie and the Gulf of Mexico represent freshwater and marine habitats where phosphorus control and stormwater runoff pose significant environmental challenges.



Figure 5.1.3.4: The uncontrolled growth of algae in this lake has resulted in an algal bloom. *Source: Jeremy Nettleton.*

Rivers and Streams

Rivers and streams are continuously moving bodies of water that carry large amounts of water from the source, or headwater, to a lake or ocean. The largest rivers include the Nile River in Africa, the Amazon River in South America, and the Mississippi River in North America.

Abiotic features of rivers and streams vary along the length of the river or stream. Streams begin at a point of origin referred to as source water. The source water is usually cold, low in nutrients, and clear. The channel (the width of the river or stream) is narrower than at any other place along the length of the river or stream. Because of this, the current is often faster here than at any other point of the river or stream.

The fast-moving water results in minimal silt accumulation at the bottom of the river or stream; therefore, the water is clear. Photosynthesis here is mostly attributed to algae that are growing on rocks; the swift current inhibits the growth of phytoplankton. An additional input of energy can come from leaves or other organic material that falls into the river or stream from trees and other plants that border the water. When the leaves decompose, the organic material and nutrients in the leaves are returned to the water. Plants and animals have adapted to this fast-moving water. For instance, leeches (*phylum Annelida*) have elongated bodies and suckers on both ends. These suckers attach to the substrate, keeping the leech anchored in place. Freshwater trout species (*phylum Chordata*) are an important predator in these fast-moving rivers and streams.

As the river or stream flows away from the source, the width of the channel gradually widens and the current slows. This slow-moving water, caused by the gradient decrease and the volume increase as tributaries unite, has more sedimentation. Phytoplankton can also be suspended in slow-moving water. Therefore, the water will not be as clear as it is near the source. The water is also warmer. Worms (*phylum Annelida*) and insects (*phylum Arthropoda*) can be found burrowing into the mud. The higher order predator vertebrates (*phylum Chordata*) include waterfowl, frogs, and fishes. These predators must find food in these slow moving, sometimes murky, waters and, unlike the trout in the waters at the source, these vertebrates may not be able to use vision as their primary sense to find food. Instead, they are more likely to use taste or chemical cues to find prey.

Wetlands

Wetlands are environments in which the soil is either permanently or periodically saturated with water. Wetlands are different from lakes because wetlands are shallow bodies of water whereas lakes vary in depth. Emergent vegetation consists of wetland plants that are rooted in the soil but have portions of leaves, stems, and flowers extending above the water's surface. There are several types of wetlands including marshes, swamps, bogs, mudflats, and salt marshes (Figure 5.1.3.5). The three shared characteristics among these types—what makes them wetlands—are their hydrology, hydrophytic vegetation, and hydric soils.



Figure 5.1.3.5: Located in southern Florida, Everglades National Park is a vast array of wetland environments, including sawgrass marshes, cypress swamps, and estuarine mangrove forests. Here, a great egret walks among cypress trees. *Source: NPS.*

Freshwater marshes and swamps are characterized by slow and steady water flow. Bogs develop in depressions where water flow is low or nonexistent. Bogs usually occur in areas where there is a clay bottom with poor percolation. Percolation is the movement of water through the pores in the soil or rocks. The water found in a bog is stagnant and oxygen depleted because the oxygen that is used during the decomposition of organic matter is not replaced. As the oxygen in the water is depleted, decomposition slows. This leads to organic acids and other acids building up and lowering the pH of the water. At a lower pH, nitrogen becomes unavailable to plants. This creates a challenge for plants because nitrogen is an important limiting resource. Some types of bog plants (such as sundews, pitcher plants, and Venus flytraps) capture insects and extract the nitrogen from their bodies. Bogs have low net primary productivity because the water found in bogs has low levels of nitrogen and oxygen.

Summary

Aquatic ecosystems include both saltwater and freshwater biomes. The abiotic factors important for the structuring of aquatic ecosystems can be different than those seen in terrestrial systems. Sunlight is a driving force behind the structure of forests and also is an important factor in bodies of water, especially those that are very deep, because of the role of photosynthesis in sustaining certain organisms. Density and temperature shape the structure of aquatic systems. Oceans may be thought of as consisting of different zones based on water depth and distance from the shoreline and light penetrance. Different kinds of organisms are adapted

to the conditions found in each zone. Coral reefs are unique marine ecosystems that are home to a wide variety of species. Estuaries are found where rivers meet the ocean; their shallow waters provide nourishment and shelter for young crustaceans, mollusks, fishes, and many other species. Freshwater biomes include lakes, ponds, rivers, streams, and wetlands. Bogs are an interesting type of wetland characterized by standing water, lower pH, and a lack of nitrogen.

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5.1.4: Climate and the Effects of Global Climate Change

5.04: Climate and the Effects of Global Climate Change

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CHAPTER OVERVIEW

Chapter 6: Speciation and Evolution of Populations (Microevolution)

Learning Objectives

- Define species and describe how scientists identify species as different
- Describe genetic variables that lead to speciation
- Identify prezygotic and postzygotic reproductive barriers
- Explain allopatric and sympatric speciation
- Describe adaptive radiation
- Explain the two major theories on rates of speciation

6.1: Species Defined

6.2: Speciation

6.3: Rates of Speciation and Extinction

6.4: Evolution of Genomes

6.5: Evolution in Populations

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6.1: Species Defined

Species Defined

- Please read and watch the following Mandatory Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 1 hour.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Confirm whether two organisms belong to the same species using the biological definition of species as a guide
- Explain how reproductive isolation can result in speciation

What is a Species?

A ***biological* species** is defined as a group of individuals that, in nature, are able to mate and produce viable, fertile offspring. There are other definitions of species but, according to the biological definition, one species is distinguished from another when, in nature, it is not possible for matings between individuals from each species to produce fertile, living offspring.

Members of the same species share both external and internal characteristics which develop from their DNA. The closer relationship two organisms share, the more DNA they have in common, just like people and their families. People's DNA is likely to be more like their father or mother's DNA than their cousin's or grandparent's DNA. Organisms of the same species have the highest level of DNA alignment and, therefore, share characteristics and behaviors that lead to successful reproduction.

Species' appearance can be misleading in suggesting an ability or inability to mate. For example, even though domestic dogs (*Canis lupus familiaris*) display phenotypic differences, such as size, build, and coat, most dogs can interbreed and produce viable puppies that can mature and sexually reproduce.



Figure 6.1.1: Dogs of different breeds still have the ability to reproduce. The (a) poodle and (b) cocker spaniel can reproduce to produce a breed known as (c) the cockapoo.

In other cases, individuals may appear similar although they are not members of the same species. For example, even though bald eagles (*Haliaeetus leucocephalus*) and African fish eagles (*Haliaeetus vocifer*) are both birds and eagles, each belongs to a separate species group. If humans were to artificially intervene and fertilize the egg of a bald eagle with the sperm of an African fish eagle and a chick did hatch, that offspring, called a hybrid (a cross between two species), would probably be infertile: unable to successfully reproduce after it reached maturity. Different species may have different genes that are active in development; therefore, it may not be possible to develop a viable offspring with two different sets of directions. Thus, even though hybridization may take place, the two species still remain separate.



(a) (b)

Figure 6.1.2: Species that appear similar may not be able to reproduce. The (a) African fish eagle is similar in appearance to the (b) bald eagle, but the two birds are members of different species.

Gene Pools

Populations of species share a **gene pool**: a collection of all the variants of genes in the species. The basis of any change in a group or population of organisms must be genetic; it is the only way to share and pass on traits. Variations within a species can only be passed to the next generation via asexual reproduction or sexual reproduction. Changes will be passed on asexually if the reproducing cell already possesses the changed trait and the offspring will be a genetic copy of the parent.

In sexual reproduction, unlike sexual reproduction, only the changed traits in gametes can be passed down to offspring. In other words, sexually-reproducing organisms can experience genetic changes in their body, or somatic, cells but if these changes do not also occur in a gamete, the changed trait will not appear in the next generation from the parents. Only heritable traits can evolve. Therefore, reproduction plays a large role for genetic changes to take root in a population or species. In summary, organisms must be able to reproduce with each other to pass new traits to offspring.

Video





In this 10.5-minute video explains the concepts of species and speciation.

Questions after watching:

There is a colony of green aphids on a tomato plant. On the tomato plant that is next to the first one, there are red aphids. The two colonies started from a third one, that was green, on another nearby plant. The green and the red aphids are distinct species, because the green aphids are attracted to green counterparts; and red ones only have interest in other red ones. Which does this example represent: Allopatric or sympatric speciation? Pre-zygotic and post-zygotic speciation?

Reproductive Isolation

Reproductive isolation, through mechanical, behavioral, and physiological barriers, is an important component of speciation. Given enough time, the genetic and phenotypic divergence between populations will affect characters that influence reproduction. In other words, if individuals of the two populations were to be brought together, mating would be improbable, but if mating did occur, offspring would be non-viable or infertile. Many factors may influence this process known as **reproductive isolation**. Reproductive isolation is the inability of two populations to interbreed with one another.

There are two different types of barriers that prevent the members of two different species from mating, to producing offspring, or having fertile offspring: prezygotic barriers and postzygotic barriers. Recall that a **zygote** is a fertilized egg: the first cell of the development of an organism that reproduces sexually. Therefore, a **prezygotic barrier** is a mechanism that blocks reproduction from taking place; this includes barriers that prevent fertilization when organisms attempt reproduction. A **postzygotic barrier** occurs after zygote formation; this includes organisms that do not survive the embryonic stage and those that are born sterile.

? Optional Activity 6.1.1

Which condition is the basis for a species to be reproductively isolated from others?

a. It does not share its habitat with related species.
b. It does not exist outside of a single habitat.
c. It does not exchange genetic information with other species.
d. It does not undergo evolutionary changes for a significant amount of time.

Answer

c. It does not exchange genetic information with other species.

Prezygotic Barriers

There are several different types of prezygotic barriers, including temporal, habitat, behavioral, gametic, and mechanical. Some of these prezygotic barriers prevent reproduction entirely. Many organisms only reproduce at certain times of the year, often just annually.

Temporal isolation

Differences in breeding schedules, called **temporal isolation**, can act as a form of reproductive isolation. For example, two species of frogs inhabit the same area, but one reproduces from January to March, whereas the other reproduces from March to May.



(a) (b)

Figure 6.1.3: These two related frog species exhibit temporal reproductive isolation. (a) Rana aurora breeds earlier in the year than (b) Rana boylii.

Habitat Isolation

In some cases, populations of a species move to a new habitat and take up residence in a place that no longer overlaps with other populations of the same species; this is called **habitat isolation**. Reproduction with the parent species ceases and a new group exists that is now reproductively and genetically independent. For example, a cricket population that was divided after a flood could no longer interact with each other. Over time, the forces of natural selection, mutation, and genetic drift will likely result in the divergence of the two groups.

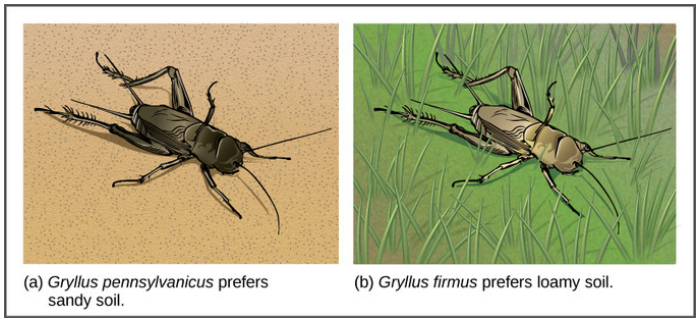


Figure 6.1.4: Speciation can occur when two populations occupy different habitats. The habitats need not be far apart. The cricket (a) *Gryllus pennsylvanicus* prefers sandy soil, while the cricket (b) *Gryllus firmus* prefers loamy soil. The two species can live in close proximity, but because of their different soil preferences, they became genetically isolated.

Behavioral Isolation

Behavioral isolation occurs when the presence or absence of a specific behavior prevents reproduction from taking place. For example, male fireflies use specific light patterns to attract females. Various species display their lights differently; if a male of one species tried to attract the female of another, she would not recognize the light pattern and would not mate with the male.

Gametic and Mechanical Barriers

Other prezygotic barriers work when differences in their gamete cells prevent fertilization from taking place; this is called a **gametic barrier**. Similarly, in some cases, closely-related organisms try to mate, but their reproductive structures simply do not fit together (**mechanical barrier**). For example, damselfly males of different species have differently-shaped reproductive organs.



Figure 6.1.5: The shape of the male reproductive organ varies among male damselfly species and is only compatible with the female of that species. Reproductive organ incompatibility keeps the species reproductively isolated.

In plants, certain structures aimed to attract one type of pollinator simultaneously prevent a different pollinator from accessing the pollen. The tunnel through which an animal must access nectar can vary in length and diameter, which prevents the plant from

being cross-pollinated with a different species.



(a) Honeybee drinking nectar from a foxglove flower

(b) Ruby-throated hummingbird drinking nectar from a trumpet creeper flower

Figure 6.1.6: Some flowers have evolved to attract certain pollinators. The (a) wide foxglove flower is adapted for pollination by bees, while the (b) long, tube-shaped trumpet creeper flower is adapted for pollination by humming birds.

Postzygotic Barriers

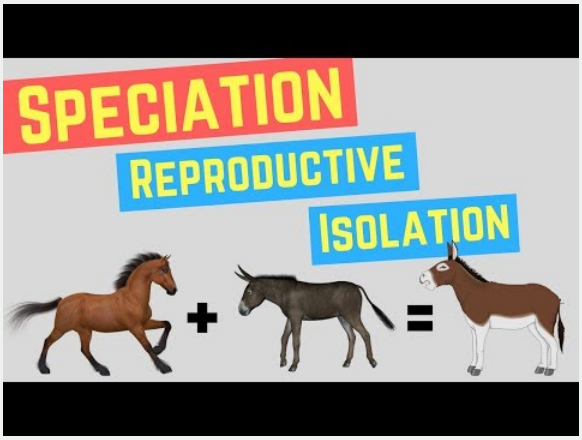
There are different types of postzygotic barriers as well, including hybrid inviability and hybrid sterility. When fertilization takes place and a zygote forms, postzygotic barriers can prevent reproduction.

Hybrid individuals in many cases cannot form normally in the womb and simply do not survive past the embryonic stages; this is called **hybrid inviability**.

In another postzygotic situation, reproduction leads to the birth and growth of a hybrid that is sterile and unable to reproduce offspring of their own; this is called **hybrid sterility**.

Video





This 3-minute video provides an overview of pre-zygotic and post-zygotic barriers to reproduction which lead to speciation.

Question after watching:

In most cases, which do you hypothesize arises first: pre-zygotic or post-zygotic barriers? Why?

Optional Activity 6.1.2

Which situation is not an example of a prezygotic barrier?

a. Two species of turtles breed at different times of year.
b. Two species of flowers attract different pollinators.
c. Two species of birds display different mating dances.
d. Two species of insects produce infertile offspring.

Answer

d. Two species of insects produce infertile offspring.

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6.2: Speciation

Speciation

- Please read and watch the following Mandatory Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 2 hours.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Define speciation and discuss the ways in which it may occur
- Give examples of allopatric speciation
- Give examples of sympatric speciation
- Discuss how the fitness of a hybrid will lead to changes in the hybrid zone over time

Speciation Defined

A biological species is a group of potentially interbreeding individuals that produce viable, fertile offspring. For the majority of sexually-reproducing species, this holds true. However, there are exceptions to this rule. Some species are similar enough that hybrid offspring are possible and may occur. The presence of hybrids in nature between similar species suggests that they may have descended from a single interbreeding species and that **speciation**, a process where a single species branches to form two or more new species, may not yet be complete.

There are mechanisms for speciation. Darwin envisioned this process as a branching event. The modern diagram shows that as one species changes over time, it branches repeatedly to form more than one new species as long as the population survives or until the organism becomes extinct.

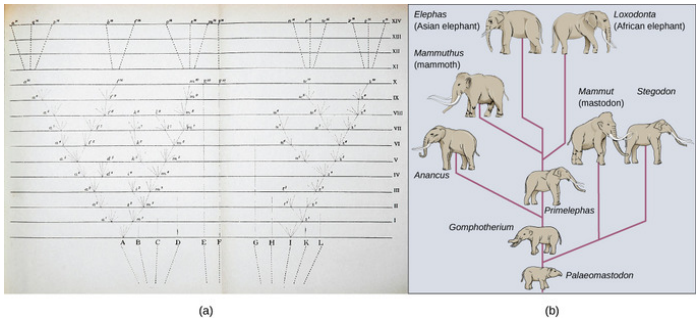


Figure 6.2.1: The only illustration in Darwin's On the Origin of Species is (a) a diagram showing speciation events leading to biological diversity. The diagram shows similarities to phylogenetic charts that are drawn today to illustrate the relationships of species. (b) Modern elephants evolved from the *Palaeomastodon*, a species that lived in Egypt 35–50 million years ago.

For speciation to occur, two new populations must be formed from one original population. They must evolve in such a way that it becomes impossible for individuals from the two new populations to interbreed. Biologists have proposed mechanisms by which this could occur that fall into two broad categories: allopatric speciation and sympatric speciation. **Allopatric speciation** (allo- = "other"; -patric = "homeland") involves geographic separation of populations from a parent species and subsequent evolution. **Sympatric speciation** (sym- = "same"; -patric = "homeland") involves speciation occurring within a parent species remaining in one location.

Biologists typically think of speciation events as the splitting of one ancestral species into two descendant species. There is no reason why there might not be more than two species formed at one time except that it is less likely; multiple events can be conceptualized as single splits occurring close in time.

Allopatric Speciation

A geographically-continuous population has a gene pool that is relatively homogeneous. Gene flow, the movement of alleles across the range of the species, is relatively free because individuals can move and then mate with individuals in their new location. Thus, the frequency of an allele at one end of the range will be similar to the frequency of the allele at the other end.

Allopatric speciation occurs when a single species becomes geographically separated from a natural or human barrier, into two or more populations. Each population evolves new and distinctive traits since gene flow is prevented. If the populations are separated for a long enough period of time, the two populations evolve along different trajectories. New alleles arise by mutation and allele frequencies gradually become different in the two populations. Typically, environmental pressures, such as climate, resources, predators, and competitors for each population will differ causing natural selection to select for different adaptations in each group.

Geographic separation of populations can occur in a variety of ways: a river forming a new branch, erosion forming a new valley, a landslide cutting off a mountain pass, or seeds floating over the ocean to an island. The nature of the geographic separation necessary to isolate populations depends on the biology of the organism and its potential for dispersal. If two flying insect populations took up residence in separate nearby valleys, chances are individuals from each population would fly back and forth, continuing gene flow. However, if two rodent populations became divided by the formation of a new lake, continued gene flow would be improbable and speciation would occur.

Scientists have documented numerous cases of allopatric speciation. For example, along the west coast of the United States, two separate sub-species of spotted owls exist. The northern spotted owl has genetic and phenotypic differences from its close relative, the Mexican spotted owl, which lives in the south. They have been separated by the emergence of mountain ranges and deserts. Additionally, scientists have found that the further the spatial distance between two groups that once were the same species, the more probable it is that speciation will occur. This seems logical because as the distance increases, the various environmental factors would generally have less in common than locations in close proximity. Consider the two owls: in the north, the climate is cooler than in the south causing the types of prey organisms in each ecosystem to differ. Also, the hunting habits and locations of each would vary. These variances can lead to evolved differences in the owls, resulting in speciation.



Figure 6.2.2: The northern spotted owl and the Mexican spotted owl inhabit geographically separate locations with different climates and ecosystems. The owl is an example of allopatric speciation.

Isolated Evolutionary Change

In isolation, changes in the gene pool can occur through some combination of natural selection and genetic drift (the bottleneck or founder effects). These factors may produce distinct subpopulations on the different islands. So long as they remain separate (allopatric) we consider them **subspecies**. In fact, they might not be able to interbreed with other subspecies but so long as we do not have evidence, we assume that they can.

How much genetic change is needed to create a new species? Perhaps not as much as you might think. Changes at one or just a few gene loci might cause speciation. For example, a single mutation altering flower color or petal shape could immediately prevent cross-pollination between the new and the parental types.

Adaptive Radiation

In some cases, a population of one species disperses throughout an area with each finding a distinct niche or isolated habitat. Over time, the varied demands of their new lifestyles lead to multiple speciation events originating from a single species. This is called **adaptive radiation** because many adaptations evolve from a single point of origin, causing the species to radiate into several new ones. Island archipelagos like the Hawaiian Islands provide an ideal context for adaptive radiation events because water surrounds each island which leads to geographical isolation for many organisms.

The Hawaiian honeycreeper illustrates one example of adaptive radiation. From a single species, called the founder species, numerous species have evolved. The response to natural selection based on specific food sources in each new habitat led to the evolution of a different beak suited to the specific food source. The seed-eating birds have a thicker, stronger beak which is suited to break hard nuts. The nectar-eating birds have long beaks to dip into flowers to reach the nectar. The insect-eating birds have beaks like swords, appropriate for stabbing and impaling insects.

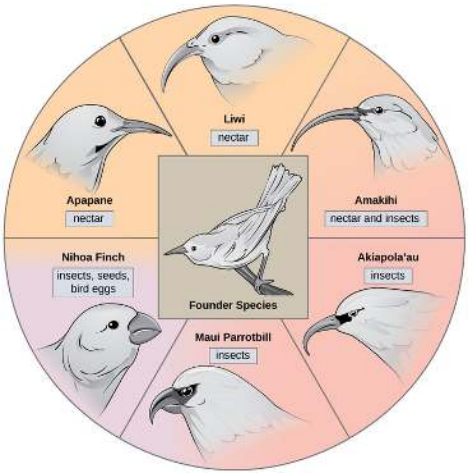


Figure 6.2.3: The honeycreeper birds illustrate adaptive radiation. From one original species of bird, multiple others evolved, each with its own distinctive characteristics.

? Optional Activity 6.2.1

Which situation would most likely lead to allopatric speciation?

a. A flood causes the formation of a new lake.
b. A storm causes several large trees to fall down.
c. A mutation causes a new trait to develop.
d. An injury causes an organism to seek out a new food source.

Answer

a. A flood causes the formation of a new lake.

Sympatric Speciation

Can divergence occur if no physical barriers are in place to separate individuals who continue to live and reproduce in the same habitat? The answer is yes. The process of speciation within the same space is called sympatric speciation. Sympatric speciation occurs when two individual populations diverge from an ancestral species without being separated geographically.

One form of sympatric speciation can begin with a large chromosomal aberration during cell division. In a normal cell division event, chromosomes replicate, pair up, and then separate so that each new cell has the same number of chromosomes. However, sometimes the pairs separate and the end cell product has too many or too few individual chromosomes in a condition called **aneuploidy**.

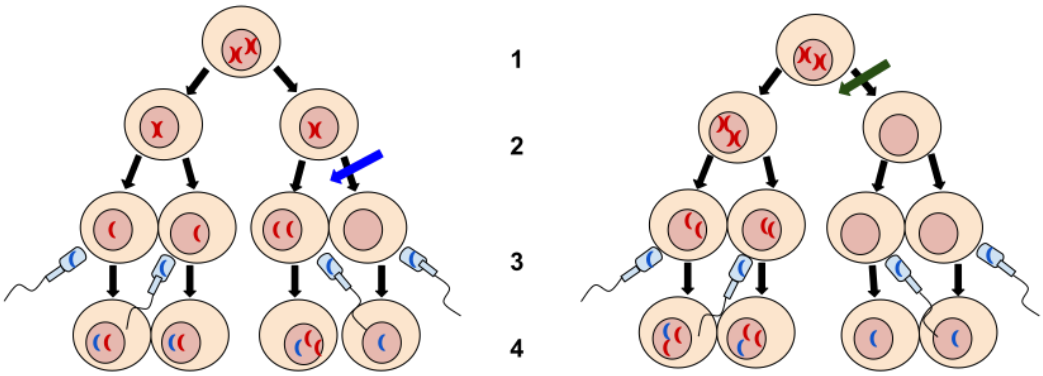


Figure 6.2.4: Aneuploidy results when the gametes have too many or too few chromosomes due to nondisjunction during meiosis. In the example shown here, the resulting offspring will have 2n+1 or 2n-1 chromosomes (Tweety207; CC-BY-SA 3.0)

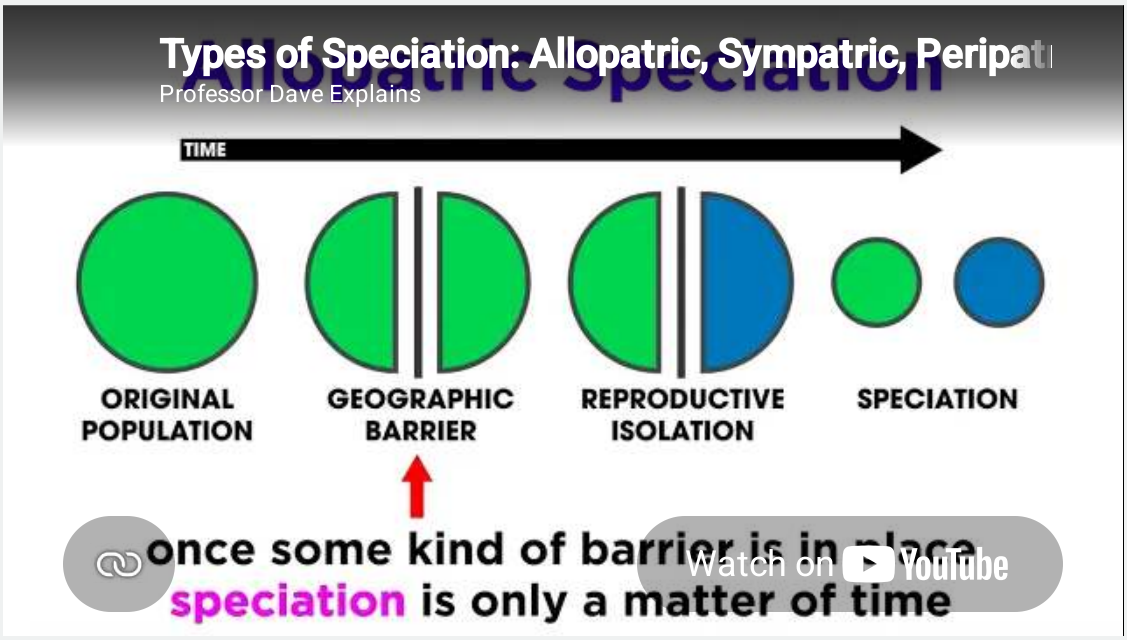
Most organisms without enough chromosomes (2n-1) will not develop. However, **polyploidy** is a condition in which a cell or organism has an extra set, or sets, of chromosomes (2n+1) and some of these organisms can develop and survive. Although polyploidy occurs occasionally in animals, it takes place most commonly in plants. The cultivated forms of wheat, cotton, and tobacco plants are all polyploids. Animals with any of the types of chromosomal aberrations described above are unlikely to survive and produce normal offspring. Scientists have discovered more than half of all plant species studied relate back to an ancestral species evolved through polyploidy. With such a high rate of polyploidy in plants, some scientists hypothesize that this mechanism takes place more as an adaptation than as an error.

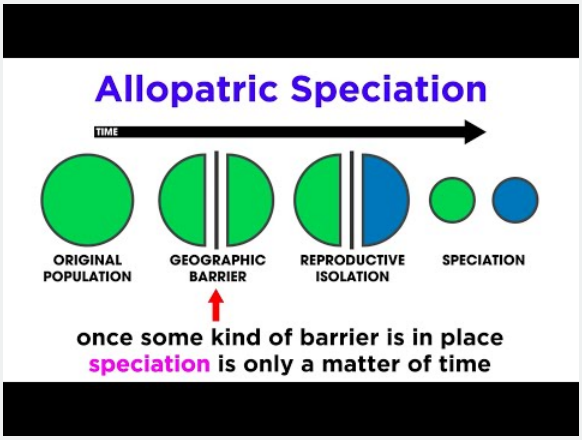
Reunion

The question of two populations' status - subspecies or true new species - is resolved if the two ever come to occupy the same territory again (become sympatric). If successful interbreeding occurs, the differences will gradually disappear, and a single population will be formed again. Speciation will not have occurred. If, on the other hand, two subspecies reunite but fail to resume breeding, speciation has occurred and they have become separate species.

The medium tree finch *Camarhynchus pauper* is found only on Floreana Island in the Galapagos. Its close relative, the large tree finch, *Camarhynchus psittacula*, is found on all the central islands of the Galapagos including Floreana. Were it not for its presence on Floreana, both forms would be considered subspecies of the same species. Because they do coexist and maintain their separate identity on Floreana, we know that speciation has occurred.

Video





Allopatric, sympatric, and parapatric speciation are all summarized in this 7-minute video.
Question after watching:
Why do island chains provide ideal conditions for adaptive radiation to occur?

Continued Isolating Mechanisms

What might keep two subpopulations from interbreeding when reunited geographically? There are several mechanisms.

Prezygotic isolating mechanisms act before fertilization occurs. On Floreana, *Camarhynchus psittacula* has a longer beak than *Camarhynchus pauper*, and the research teams led by Peter and Rosemary Grant have demonstrated that beak size is an important criterion by which Darwin's finches choose their mates. Two subpopulations may occupy different habitats in the same area and thus fail to meet at breeding time. In plants, a shift in the time of flowering can prevent pollination between the two subpopulations. Structural differences in the sex organs may become an isolating mechanism. The sperm may fail to reach or fuse with the egg.

Postzygotic isolating mechanisms act even if fertilization does occur. Even if a zygote is formed, genetic differences may have become so great that the resulting hybrids are less viable or less fertile than the parental types. The sterile mule produced by mating a horse with a donkey is an example. Sterility in the males produced by hybridization is more common than in females. In fact, it is the most common postzygotic isolating mechanism. When *Drosophila melanogaster* attempts to mate with its relative *Drosophila simulans*, no viable males are even produced. Mutations in a single gene are responsible.

Speciation by Hybridization

Speciation occurs over a span of evolutionary time. Over time, two species may further diverge or reconnect, depending on the fitness strength and the reproductive barriers of the hybrids. When a new species arises, there is a transition period during which the closely-related species continue to interact.

After speciation, two species may recombine or even continue interacting indefinitely. Individual organisms will mate with any nearby individual with which they are capable of breeding. An area where two closely-related species continue to interact and reproduce, forming hybrids, is called a **hybrid zone**. Over time, the hybrid zone may change depending on the fitness strength and the reproductive barriers of the hybrids.

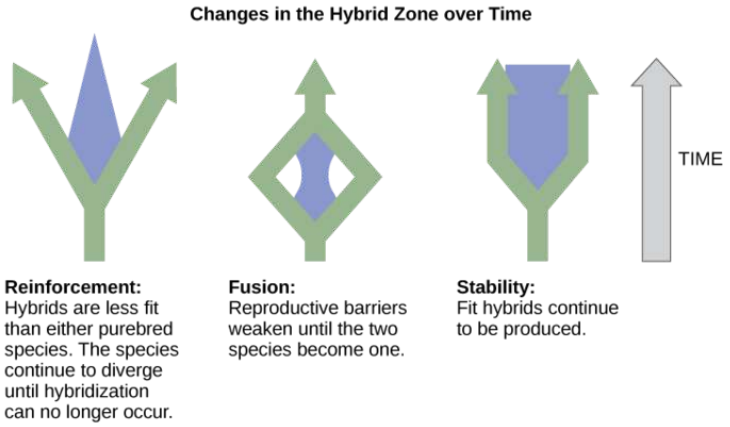


Figure 6.2.7: After speciation has occurred, the two separate-but-closely-related species (green lines) may continue to produce offspring in an area called the hybrid zone (blue area). The thicker the blue line, the more hybridization occurs between the two species.

Reinforcement

When two species that have separated in allopatry become reunited, their prezygotic and postzygotic isolating mechanisms may become more stringent than those between the same species existing apart from each other. This phenomenon is called **reinforcement**. It arises from natural selection working to favor individuals that avoid interspecific matings, which would produce less-fit hybrids, when the two species are first reunited.

ybrids can have less fitness, more fitness, or about the same fitness level as their purebred parents. Usually, hybrids tend to be less fit; therefore, reproduction to produce hybrids will diminish over time, which nudges the two species to diverge further. This term is used because the low success of the hybrids reinforces the original speciation. If the hybrids are less fit than the parents, reinforcement of speciation occurs, and the species will continue to diverge until they can no longer mate and produce viable offspring.

If the hybrids are as fit or more fit than the parents, or the reproductive barriers weaken, the two species may fuse back into one species. For a hybrid form to persist, it will generally have to be able to exploit the available resources better than either parent species, with which, in most cases, it will have to compete.

Over time, the hybrids themselves can become separate species. Reproductive isolation between hybrids and their parents was once thought to be particularly difficult to achieve; thus, hybrid species were thought to be extremely rare. With DNA analysis becoming more accessible in the 1990s, hybrid speciation has been shown to be a fairly common phenomenon, particularly in plants.

Video





This 8.5-minute animated video explains how species are crated using a fictional bird species that lands on a volcanic island (which mirrors what happened on the Galapagos Islands).

Question after watching:

Given what you have learned about the process of speciation, why do humans not have any sister species? Propose a hypothesis…

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Rates of Speciation and Extinction

- Please read and watch the following Mandatory Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 30 minutes.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
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Learning Objectives

- Explain how the interaction of an organism's population size in association with environmental changes can lead to different rates of speciation

Varying Rates of Speciation

Scientists around the world study speciation, documenting observations both of living organisms and those found in the fossil record. As their ideas take shape and as research reveals new details about how life evolves, they develop models to help explain rates of speciation. In terms of how quickly speciation occurs, two patterns are currently observed: the gradual speciation model and the punctuated equilibrium model.

In the **gradual speciation** model, species diverge gradually over time in small steps. In the **punctuated equilibrium** model, a new species changes quickly from the parent species and then remains largely unchanged for long periods of time afterward. This early change model is called punctuated equilibrium, because it begins with a punctuated or periodic change and then remains in balance afterward. While punctuated equilibrium suggests a faster tempo, it does not necessarily exclude gradualism.

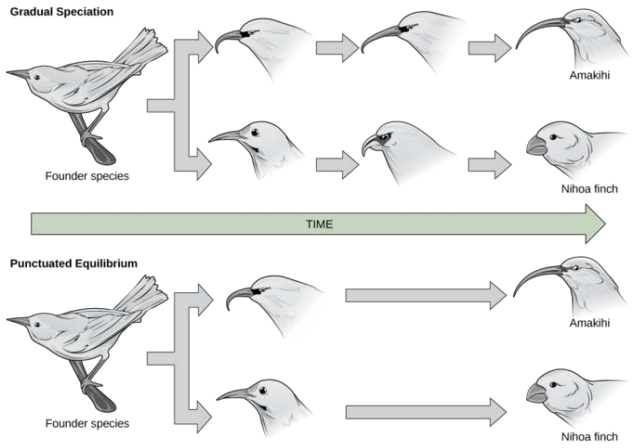


Figure 6.3.1: In (a) gradual speciation, species diverge at a slow, steady pace as traits change incrementally. In (b) punctuated equilibrium, species diverge quickly and then remain unchanged for long periods of time.

British Columbia Connections 6.3.1

Evolutionary biologist Stephen J. Gould used the formations of the Burgess Shales, between Golden, British Columbia and Banff, Alberta, to support his hypothesis of the punctuated equilibrium model. The Burgess Shales are one of the foremost places in the world to study the fossils of the Cambrian Explosion of life from 550 million years ago.

The Burgess Shales foundation website: https://www.burgess-shale.bc.ca/the-cambrian-explosion-and-the-burgess-shale/

American Museum of Natural History website on Burgess Shales: https://www.amnh.org/research/paleontology/collections/fossil-invertebrate-collection/trilobite-website/niles-eldredge-trilobites-punctuated-equilibria

Canadian Encyclopedia entry on Burgess Shales: https://www.thecanadianencyclopedia.ca/en/article/burgess-shale-fossils

The primary influencing factor on changes in speciation rate is environmental conditions. Under some conditions, selection occurs quickly or radically. Consider a species of snails that had been living with the same basic form for many thousands of years. Their fossils would appear similar for a long time. When a change in the environment takes place, such as a drop in the water level, a small number of organisms are separated from the rest in a brief period of time, essentially forming one large and one tiny population. The tiny population faces new environmental conditions. Because its gene pool quickly became so small, any variation that aids in surviving the new conditions becomes the predominant form. More on speciation (and extinction) is discussed in Unit 3.3.1.

? Optional Activity 6.3.1

Which of the following statements is false?

a. Punctuated equilibrium is most likely to occur in a small population that experiences a rapid change in its environment.
b. Punctuated equilibrium is most likely to occur in a large population that lives in a stable climate.
c. Gradual speciation is most likely to occur in species that live in a stable climate.
d. Gradual speciation and punctuated equilibrium both result in the divergence of species.

Answer

B. Punctuated equilibrium is most likely to occur in a large population that lives in a stable climate.

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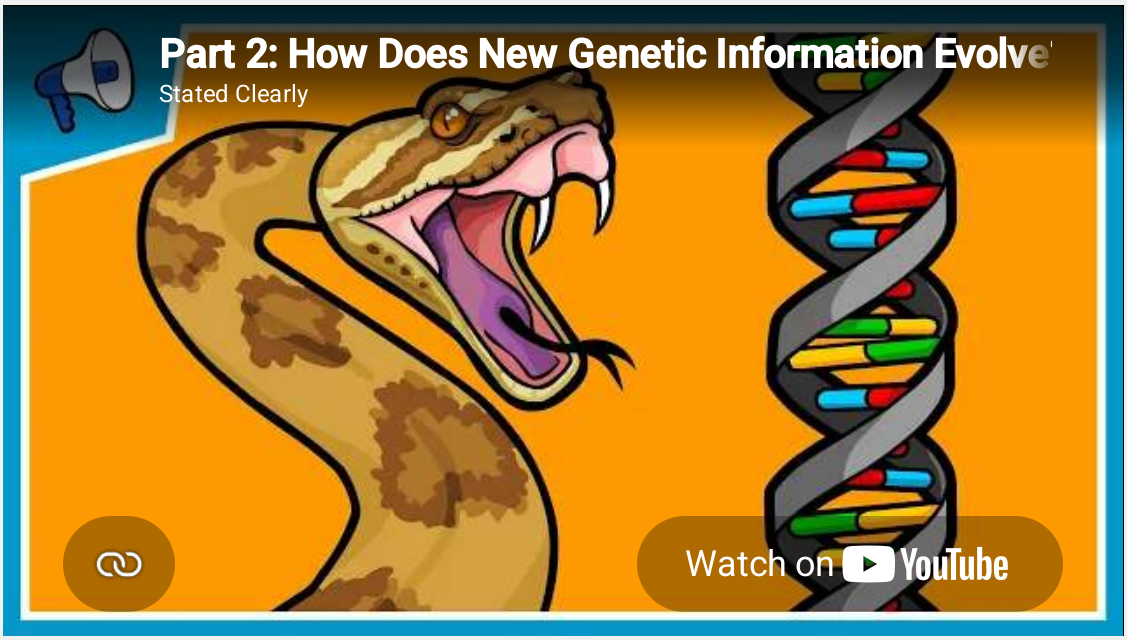
Evolution of Genomes

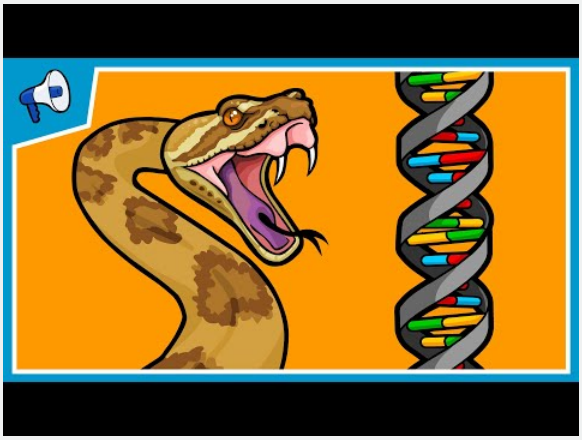
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Learning Objectives

- Identify how variations in the size and number of genes in different species can impact evolution;
- Explain the importance of genomic changes in an evolutionary context;
- Recognize the evolutionary implications of observed genome similarities between distant species.

Video





This 9-minute video provides an overview of how the genes and genome of a species can change over time to lead to different species.

Questions after watching: How can a gene duplication event fuel evolution? Can you think of another example where something was duplicated and then repurposed by evolution?

Genetic Diversity

Genetic variation is essential for a species to evolve in response to environmental change, including any variation in nucleotides, genes, chromosomes, or genomes of organisms. Each of these levels of genetic diversity adds to the capacity of a population to evolve.

Variations in the Number of Genes

DNA is contained in the chromosomes present within the cell; some chromosomes are contained within specific organelles in the cell (for example, the chromosomes of mitochondria and chloroplast). A gene is a discrete section of a chromosome that codes for one or more proteins. Each gene is a hereditary section of DNA that occupies a specific place on the chromosome and controls a particular characteristic of an organism. Genetic diversity at its most elementary level is represented by differences in the sequence of nucleotides (with one of the following bases: adenine, cytosine, guanine) that form DNA (deoxyribonucleic acid) within the cells of the organism. During sexual reproduction, offspring inherit alleles from both parents. These inherited alleles might be slightly different, especially if there has been migration or hybridization of organisms. Also, when the offspring's chromosomes are copied after fertilization, genes can be exchanged in a process called sexual recombination. Helpful or silent mutations and sexual recombination may allow the evolution of new characteristics.

Sometimes whole genes are duplicated, or deleted. This results in an organism having more or fewer copies of that gene than others. The effect on the phenotype may be to increase or decrease the gene product's function (e.g., if the gene encoded a protein that makes pigment, and now the organism has two genes encoding pigment, the organism may now be twice as pigmented as its parents with only one copy of the gene). Natural selection may then select for or against organisms with this altered number of gene copies.

Sometimes there is no immediate effect of gene duplication on phenotype. The additional copy of the gene may accumulate mutations without deleterious effects on the organism. These mutations will likely modify the gene product's function if it is transcribed. In doing this, the gene may acquire slightly different abilities, such as the factor X blood clotting example in the video above.

Variations in the Number of Chromosomes

Many organisms are diploid, having two sets of chromosomes, and therefore two copies (called alleles) of each gene. However, some organisms can be haploid, triploid, or tetraploid (having one, three, or four sets of chromosomes respectively). Within any single organism, there may be variation between the two (or more) alleles for each gene. This variation is introduced either through mutation of one of the alleles or as a result of recombination during sexual reproduction.

During replication events, there can be mutations that involve whole chromosomes or whole chunks of chromosomes. Some mutations duplicate a whole chromosome (a whole stretch of DNA with many genes); some may delete a large portion. Some rearrange chromosomes, keeping all of the DNA information but putting it in different places in the genome. It turns out that in some instances, the location matters because it contains sites that initiate and control transcription. In bacteria, this can matter because one transcription factor can control the transcription of many genes in a row.

Changes in chromosome number or structure can affect many genes at the same time. Like changes in individual genes, this can result in some immediate effects because of the change in the number of genes producing the gene products (proteins). Or there can be little to no immediate effect, but the extra copy gives rise to "spare copies" that are free to mutate and acquire new abilities and functions.

Variation in Genome Size

A **genome** is the total genetic information of a cell or organism. The evolution of the genome is characterized by the accumulation of changes. Analysis of genomes and their changes in sequence or size over time involves various fields.

Genome size is usually measured in base pairs (or bases in single-stranded DNA or RNA). Different species can have different numbers of genes within the entire DNA or genome of the organism. Gene number is the main factor influencing the size of the

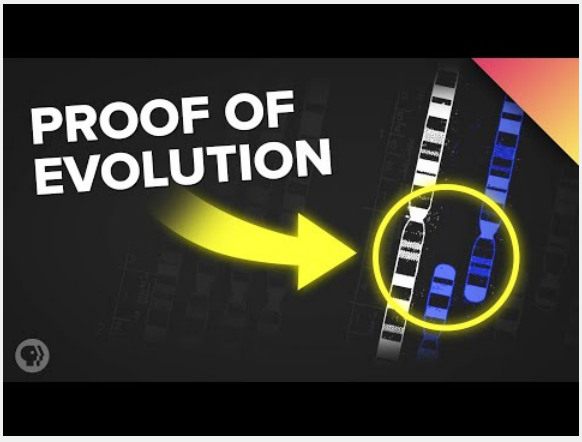
prokaryotic genome. However, a greater total number of genes might not correspond with greater complexity in the phenotype (behavior, structure, or function) of eukaryotes.

For example, the predicted size of the human genome is not much larger than the genomes of some invertebrates and is far smaller than some species of ferns. However, in humans, more proteins are encoded *per gene* than in other species. In eukaryotic organisms, this is an observed paradox: the number of genes that make up the genome does not correlate with genome size. In other words, the genome size is much larger than would be expected given the total number of protein-coding genes.

Larger amounts of genetic information may allow for more variation in the overall genome, conferring additional adaptability to environmental change. It may also play a role in speciation. On the other hand, longer genomes take more energy and time to duplicate, so there is an evolutionary trade-off.

Video





In this 8-minute video, evidence of human evolution in the human genome is demonstrated.
Question after watching:
What are three lines of evidence from the human genome of our evolutionary past?

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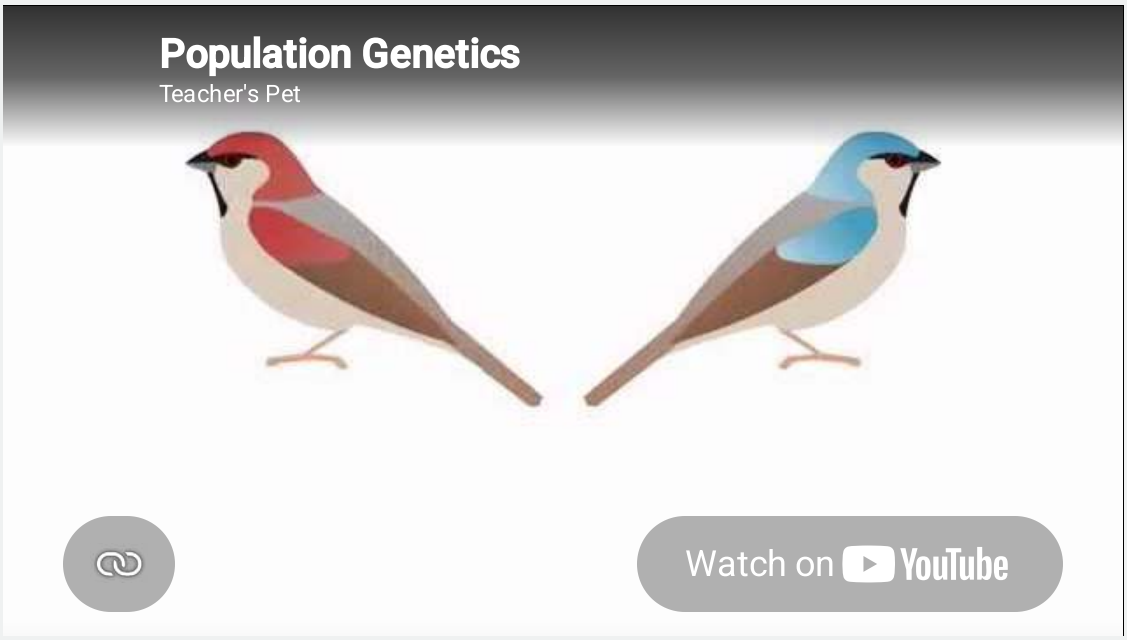
Evolution in Populations

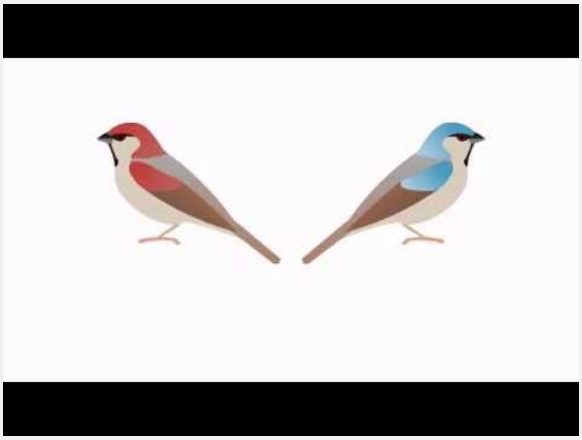
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Learning Objectives

- Describe how mutations, natural selection, genetic drift, and gene flow can modify the genes in a population.
- Define a population gene pool.
- Explain how the size of the gene pool can affect the evolutionary success of a population.
- Use the Hardy-Weinberg equation to calculate allelic and genotypic frequencies in a population.
- Use the results of a Hardy-Weinberg analysis to determine whether evolution is taking place in a population.

Video





This short 3-minute video provides a good introduction to population genetics and its relationship to evolution. Question after watching: At 2:13, the slide shows 4 elements that the narrator says are the elements that make up the gene pool. She is incorrect on one count. Which one? And why? Integrate some of the concepts you have learned previously with the ones introduced in this video. Describe how something like a genetic bottleneck might create changes in a population's gene pool.

The Evolution of Populations

According to evolutionary theory, every organism from humans to beetles to plants to bacteria shares a common ancestor (Figure 6.5.1). Millions of years of evolutionary pressure caused some species to go extinct while others survived. Earth is filled with more diversity now than at any other point in its history. All life is still connected, however. For example, all organisms are composed of cells and use DNA. The theory of evolution gives us a unifying theory to explain what caused the diversity of species that now exist.



Figure 6.5.1: Evolution has resulted in living things that may be single-celled or complex, multicellular organisms. They may be plants, animals, fungi, bacteria, or archaea. This diversity results from evolution.

Genetic Variation in Populations

A **population** is a group of individuals that can all interbreed, often distinguished as a species. These individuals can share genes and pass on combinations of genes to the next generation, containing all of the variation in its gene pool. The process of evolution occurs *only* in populations and not in individuals. A single individual cannot evolve alone; evolution is the process of changing the gene frequencies within a gene pool. Five forces can cause genetic variation and evolution in a population: mutations, genetic recombination, natural selection, genetic drift, and gene flow. Refresh your understanding of these concepts in Section 2.2.

Allele Frequencies

A gene for a particular characteristic may have several variations called **alleles**. These variations code for different traits associated with that characteristic. The **allele frequency** (or gene frequency) is the rate at which a specific allele exists within a population. Allele frequencies can be expressed as a decimal or as a percent and always add up to 1, or 100 percent, of the total population. The **gene pool** is the sum of all the alleles at all genes in a population. When calculating the frequency of an allele in a population, remember that for diploid organisms like humans and animals, there are two alleles of each gene in the population.

For example, in the ABO blood type system in humans, three alleles (I^A, I^B, or i) determine the particular blood-type of red blood cells (Figure 6.5.2). Individuals who are phenotypically blood group "A" have the ability to attach certain sugars to the surface of red blood cells. The genotype that confers that ability are I^AI^A or I^Ai. Individuals who are blood group "B" have a different allele of that gene that codes for a protein that adds a different type of sugar on the surface of blood cells. The alleles is labeled I^B, so homozygous I^BI^B or heterozygous I^Bi have that blood type. Individuals who have one allele of each, I^A and I^B can add both sugars on the surface of their blood cells. Finally, people who lack either of these alleles encode an enzyme that cannot add either sugar types and so are blood type "O" and have homozygous alleles ii.

A diploid organism can only carry two alleles for a particular gene. In human blood type, the combinations are composed of two alleles such as I^AI^A or I^AI^B. Although each organism can only carry two alleles, more than those two alleles may be present in the

larger population. In a population of fifty people where all the blood types are represented, there may be more I^A alleles than i alleles.

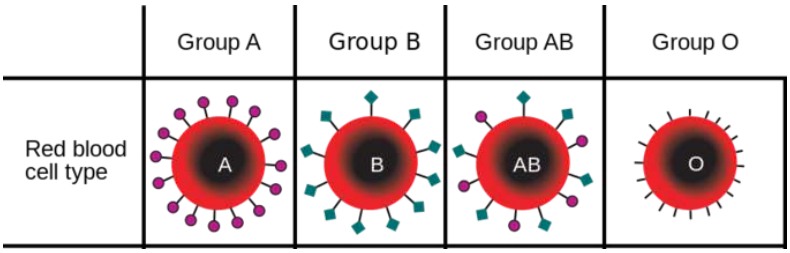
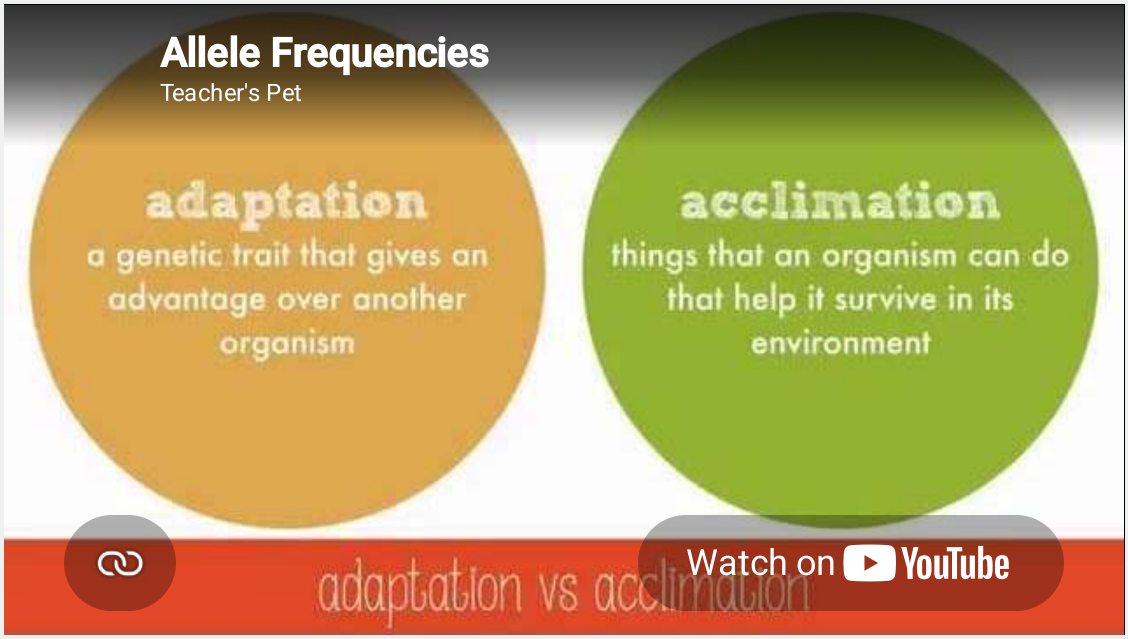


Figure 6.5.2: In humans, each blood type corresponds to a combination of two alleles. Human blood types are A, B, AB, and O.

Using the ABO blood type system as an example, the frequency of one of the alleles, for example I^A, is the number of copies of that allele divided by all the copies of the ABO gene in the population, i.e. all the alleles. In a sample population of humans, the frequency of the I^A allele might be 0.26, which would mean that 26% of the chromosomes in that population carry the I^A allele. If we also know that the frequency of the I^B allele in this population is 0.14, then the frequency of the i allele is 0.6, which we obtain by subtracting all the known allele frequencies from 1 (thus: 1 – 0.26 – 0.14 = 0.6). A change in any of these allele frequencies over time would constitute evolution in the population.

Video





This 4.5-minute video explains how to calculate allelic frequencies in a population. It will also introduce the concept of HW equilibrium, which we will explore later in this chapter.
Question after watching:
How would you explain the concept of allele frequencies to someone not in your course?

Case of the Hamsters (Part I) - Establishing Alleles

Our case begins with hypothetical species of hamster that carries two alleles for coat color in the population: black which is dominant (**B**) and grey, which is recessive (**b**).

Using a Punnett square, if two black hamsters mate that are heterozygous (e.g., **Bb**) (Table 6.5.1), we find that

- 25% of their offspring are homozygous for the dominant allele (**BB**)
- 50% are heterozygous like their parents (**Bb**)
- 25% are homozygous for the recessive allele (**bb**) and thus, unlike their parents, express the recessive phenotype.

Note

Find a refresher on Punnett squares here: Punnett Squares

This is what Mendel found when he crossed monohybrids. It occurs because meiosis separates the two alleles of each heterozygous parent so that 50% of the gametes will carry one allele and 50% the other and when the gametes are brought together at random, each **B** (or **b**)-carrying egg will have a 1 in 2 probability of being fertilized by a sperm carrying **B** (or **b**).

Table 6.5.1. Results of random union of the two gametes produced by two individuals, each heterozygous for a given trait. As a result of meiosis, half the gametes produced by each parent with carry allele **B**; the other half allele **b**.

	0.5 **B**	0.5 **b**
0.5 **B**	0.25 **BB**	0.25 **Bb**
0.5 **b**	0.25 **Bb**	0.25 **bb**

However, the frequency of two alleles in an *entire population* of organisms is unlikely to be exactly the same. We will return to this case in a moment.

The Hardy-Weinberg Principle: A Theory of Population Evolution

Theoretical Background

In the early twentieth century, English mathematician Godfrey Hardy and German physician Wilhelm Weinberg stated the principle of equilibrium to describe the population's genetic makeup. The theory, which later became known as the Hardy-Weinberg principle of equilibrium, states that a population's allele and genotype frequencies are inherently stable— unless some kind of evolutionary force is acting upon the population, neither the allele nor the genotypic frequencies would change.

Ultimately, the Hardy-Weinberg principle models a population without evolution under the following conditions:

1. no mutations
2. no immigration/emigration
3. no natural selection
4. only random matings
5. a large population

In theory, if a population is at equilibrium—that is, there are no evolutionary forces such as natural selection, mutation, etc. acting upon it—generation after generation would have the same gene pool and genetic structure, and the allele frequencies would stay the same over time. This is because all of the alleles would have an equal chance of being passed to the next generation and the ratios would remain constant.

Of course, even Hardy and Weinberg recognized that no natural population is immune to evolution. Evolution involves changes in the gene pool. Populations in nature are constantly changing in genetic makeup due to drift, mutation, possibly migration, and selection.

Hardy-Weinberg Principle

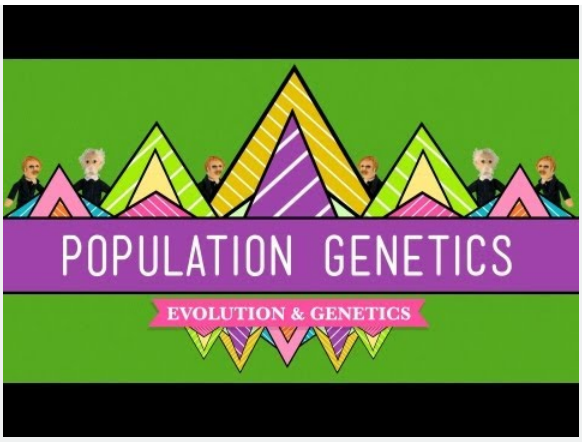
So long as certain conditions are met (discussed below), allele frequencies and genotype ratios in a randomly-breeding population remain constant from generation to generation. This is known as the Hardy-Weinberg Principle.

As a result, the only way to determine the exact distribution of phenotypes in a population is to go out and count them. A population in Hardy-Weinberg equilibrium shows no change. What the law tells us is that populations are able to maintain a reservoir of variability so that if future conditions require it, the gene pool can change. If the frequencies of alleles or genotypes deviate from the value expected from the Hardy-Weinberg equation, then the population is evolving.

When populations are in the Hardy-Weinberg equilibrium, the allelic frequency is stable from generation to generation and the distribution of alleles can be determined. If the allelic frequency measured in the field differs from the predicted value, scientists can make inferences about what evolutionary forces are at play. However, what ultimately interests most biologists is not the frequencies of different alleles, but the frequencies of the resulting genotypes, from which scientists can surmise phenotype distribution.

Video





This 11-minute Crash Course video provides an overview of population genetics in a humorous manner.

Questions after watching:

In this video, the narrator says there are 5 ways to alter the gene pool of a population. Yet, above, we only introduced 4 mechanisms to alter the allelic frequency of a population. Both are correct. Explain how this could be. What's another way to say that a population is in Hardy-Weinberg equilibrium?

Applying Hardy-Weinberg

While no population can satisfy those conditions, the principle offers a useful model against which to compare real population changes. The genetic variation of natural populations is constantly changing from genetic drift, gene flow, mutation, migration, and natural selection. **Population genetics** is the study of the distributions and changes of allele frequency in a population. In population genetics, evolution is defined as a change in the frequency of an allele in a population.

The Hardy-Weinberg principle gives scientists a mathematical baseline of a non-evolving population to which they can compare observable populations in the field or laboratory to determine whether they are evolving. If scientists record allele frequencies over time and then calculate the expected frequencies based on Hardy-Weinberg values, then scientists can detect when a population deviates from HW expectations and therefore confirm that the population is evolving. The Hardy-Weinberg principle states that a population's allele and genotype frequencies will remain constant in the absence of evolutionary mechanisms. Note that this conclusion does not inform the researcher as to which mechanism of allelic frequency change is at play, only that allelic frequencies are changing (i.e. that evolution is occurring).

Working under this theory, population geneticists represent different alleles as different variables in their mathematical models (Figure 6.5.3). The variable p, for example, represents the frequency of a particular allele, say A for the trait of tall plants in Mendel's peas, while the variable q represents the frequency of alleles that confer the short plant trait, a. If these are the only two possible alleles for a given locus in the population, then $p + q = 1$. In other words, all the p alleles and all the q alleles comprise all of the alleles for that locus in the population.

If we observe the phenotype, we can know only the homozygous recessive allele's genotype. The Hardy-Weinberg calculations provide an estimate of the remaining genotypes. Since each individual carries two alleles per gene, if we know the allele frequencies (p and q), predicting the genotypes' frequencies is a simple mathematical calculation to determine the probability of obtaining these genotypes if we draw two alleles at random from the gene pool, as we will see below.

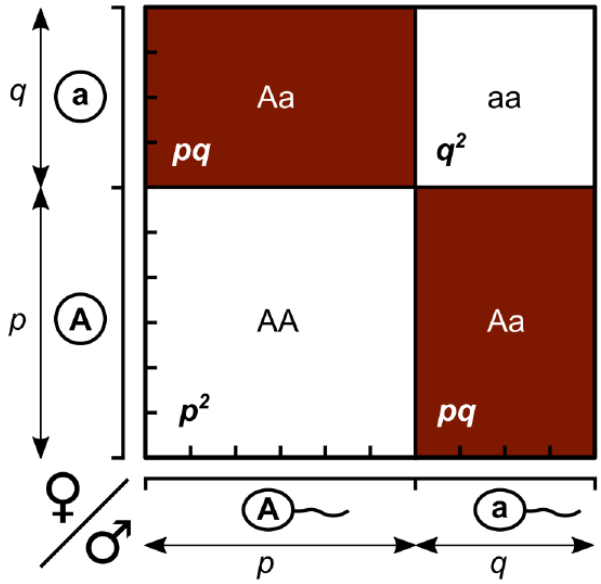


Figure 6.5.3: Hardy-Weinberg and the Punnett Square. (CC0 1.0)

Calculating Gene Pools and Genotype Frequencies

Gene pools

The total number of genes in a population is its gene pool.

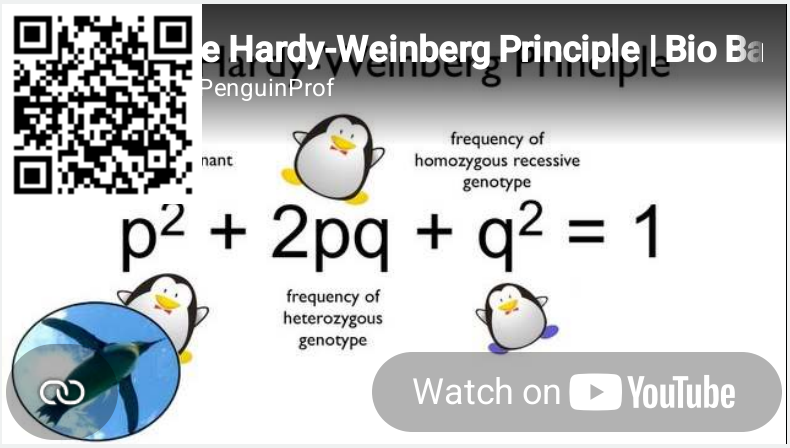
- Let p represent the frequency of the dominant allele in the gene pool and q the frequency of the recessive allele in the gene pool.
- Because p and q together equal all of the alleles in the gene pool, $p + q = 1$

Genotype frequencies

- Homozygous dominant individuals have two p alleles. Their genotype frequency can be determined by p x p or p^2.
- Similarly, homozygous recessive individuals have two q alleles. Their genotype frequency can be determined by q x q or q^2
- Heterozygous individuals are $2pq$. Their genotype frequency can be determined by 2 x p x q or $2pq$. [There are two possible types of heterozygous unions: pq and qp. Therefore, we calculate 2 x p x q]
- Because p^2, q^2, and $2pq$ together equal all of the genotypes in a population, $p^2 + 2pq + q^2 = 1$

If any one of the variables above is known, the allele frequency or genotype frequencies can be calculated. We will revisit our case study below to see how these equations are put into practice by scientists to understand whether evolution is occurring in a population.

Video



This 11-minute video describes how to calculate allele and gene pool frequencies with the Hardy-Weinberg equations. Examples and practice equations are given below.

Case of the Hamsters (Part II) - Calculating Allele and Genotype Frequency

The frequency of two alleles in an *entire population* of organisms is unlikely to be exactly the same as we saw in the Punnett square of Part 1. However, from a given genotype (or recessive phenotypes since that genotype is known), we can infer the frequencies of the alleles in a population.

Since each diploid individual carries two alleles per gene, we can predict the frequencies of these genotypes using a probability matrix Table 6.5.2. If two alleles are drawn at random from the gene pool, we can determine the probability of each genotype. We are now calculating percentages based on overall populations (not individual pairings like a Punnett square). In this type of probability matrix, *all* of the alleles that can mix in a population to produce the next generation are represented.

1. Revisiting our hypothetical case of a population of hamsters, for the purposes of example, we will establish that 80% of all the gametes in the population carry a dominant allele for black coat (B) and 20% carry the recessive allele for gray coat (b). So, p = 0.8 and q = 0.2.
2. We can now use those two values to calculate the genotype frequencies where p^2 = 0.64 and q^2 = 0.04
3. The equation above states $p^2 + 2pq + q^2 = 1$. We have calculated p^2 and q^2 but need to now solve for $2pq$.
4. We can determine from our calculations that 0.64 + $2pq$ + 0.04 = 1
5. From there 0.64 + 0.04 + $2pq$ = 1
6. And 0.68 + $2pq$ = 1
7. So, $2pq$ = 1 - 0.68 = 0.32 or 32%

Therefore, in this case, the random union of these allele frequencies will produce a generation:

- 64% homozygous for BB
- 32% Bb heterozygotes
- 4% homozygous (bb) for gray coat

So 96% of the next generation will have black coats; only 4% gray coats. If you notice, this is the same phenotype ratio as the initial population. No change has occurred, which is explained in more detail below.

Table 6.5.2. Results of random union of the gametes produced by an entire population with a gene pool containing 80% **B** and 20% **b**.

	0.8 **B**	0.2 **b**
0.8 **B**	0.64 **BB**	0.16 **Bb**
0.2 **b**	0.16 **Bb**	0.04 **bb**

Hardy-Weinberg and Selection Pressures

Natural selection affects allele and genotype frequency. If an allele confers a phenotype that enables an individual to better survive or have more offspring, the frequency of that allele will increase because the individual carrying these alleles will be effective at transferring them into the next generation. Because many of those offspring will also carry the beneficial allele and, therefore, the phenotype, they will have more offspring of their own that also carry the allele. Over time, the allele will spread throughout the population and may become fixed: every individual in the population carries the allele. If an allele is dominant but detrimental, it may be swiftly eliminated from the gene pool when the individual with the allele does not reproduce. However, a detrimental recessive allele can linger for generations in a population, hidden by the dominant allele in heterozygotes. In such cases, the only individuals to be eliminated from the population are those unlucky enough to inherit two copies of such an allele.

So, will deleterious alleles eventually disappear? No. Let's see why using our case study.

Imagine that the grey coat color carries with it some sore of negative selection pressure. If we calculate the allele frequencies, using our genotype frequencies from Table 6.5.2 above, we can recalculate how much of the population carries the dominant allele and what percentage carries the recessive allele.

- All the gametes formed by BB hamsters will contain allele B (0.64) as will one-half the gametes formed by heterozygous (Bb) hamsters (0.32/2).
  - So, 80% (0.64 + (0.32*1/2)) of the pool of gametes formed by this generation will contain B.
- All the gametes of the gray (bb) hamsters (4%) will contain b (0.04) but one-half of the gametes of the heterozygous hamsters will as well (0.32/2).
  - So 20% (0.04 + (0.32*1/2)) of the gametes will contain b.

What we find from this analysis is that in the parental generation, 80% of the alleles were B and 20% of the alelles were b. The organisms of that population mated and produced generation 2. This was a random sampling event of the alleles in the parental gene pool. In the generation 2 alleles, we find the 80% of the alleles are B and 20% are b. This is identical to the parental allelic frequency.

The proportion of allele b in the population has remained the same from the parent generation. The heterozygous hamsters ensure that each generation will contain 4% gray hamsters. Recessive genes do not tend to be lost from a population no matter how small their representation. If recessive alleles were continually tending to disappear, the population would soon become homozygous. Under Hardy-Weinberg conditions, genes that have no present selective value will nonetheless be retained.

If an allele confers a phenotype that enables an individual to better survive or have more offspring, the frequency of that allele will increase because the individual carrying these alleles will be effective at transferring them into the next generation. Because many of those offspring will also carry the beneficial allele and, therefore, the phenotype, they will have more offspring of their own that also carry the allele. Over time, the allele will spread throughout the population and may become fixed: every individual in the population carries the allele. If an allele is dominant but detrimental, it may be swiftly eliminated from the gene pool when the individual with the allele does not reproduce. However, a detrimental recessive allele can linger for generations in a population, hidden by the dominant allele in heterozygotes. In such cases, the only individuals to be eliminated from the population are those unlucky enough to inherit two copies of such an allele.

? Optional Activity 6.5.1

In the Punnett square in Figure 6.5.4, an individual pea plant could be pp (YY), and thus produce yellow peas; pq (Yy), also yellow; or qq (yy), and thus produce green peas. If 9% of the overall plants in a population produce green peas, what percentage of pea plants are heterozygous for pea color?

Answer (Click here)

According to the Hardy-Weinberg principle, the variable *p* represents the frequency of a particular allele, usually a dominant one. For example, assume that *p* represents the frequency of the dominant allele, Y, for yellow pea pods. The variable *q* represents the frequency of the recessive allele, y, for green pea pods. If p and q are the only two possible alleles for this characteristic, then the sum of the frequencies must add up to 1, or 100 percent. We can also write this as $p + q = 1$. If the frequency of the Y allele in the population is 0.6, then we know that the frequency of the y allele is 0.4.

In the example, our three genotype possibilities are: pp (YY), producing yellow peas; pq (Yy), also yellow; or qq (yy), producing green peas. The frequency of homozygous dominant individuals is p^2; the frequency of heterozygous individuals is 2pq; and the frequency of homozygous recessive individuals is q^2. If p and q are the only two possible alleles for a given trait in the population, these genotypes frequencies will sum to one: $p^2 + 2pq + q^2 = 1$.

In our example, the possible genotypes are homozygous dominant (YY), heterozygous (Yy), and homozygous recessive (yy). If we can only observe the phenotypes in the population, then we know only the recessive phenotype (yy). For example, in a garden of 100 pea plants, 86 might have yellow peas and 16 have green peas. We do not know how many are homozygous dominant (Yy) or heterozygous (Yy), but we do know that 16 of them are homozygous recessive (yy).

Therefore, by knowing the recessive phenotype and, thereby, the frequency of that genotype (16 out of 100 individuals or 0.16), we can calculate the number of other genotypes.

1. If q^2 represents the frequency of homozygous recessive plants, then $q^2 = 0.16$.

2. Therefore, q = 0.4 (the square root of 0.16 is 0.4...we cannot have a negative number when working with allele frequencies).
3. Because p + q = 1 and q = 0.4, then 1 – 0.4 = p.
4. p = 0.6.
5. The frequency of homozygous dominant plants (p^2) is $(0.6)^2 = 0.36$. So, out of 100 individuals, there are 36 homozygous dominant (YY) plants.
6. The frequency of heterozygous plants (2pq) is 2(0.6)(0.4) = 0.48. Therefore, 48 out of 100 plants are heterozygous yellow (Yy).

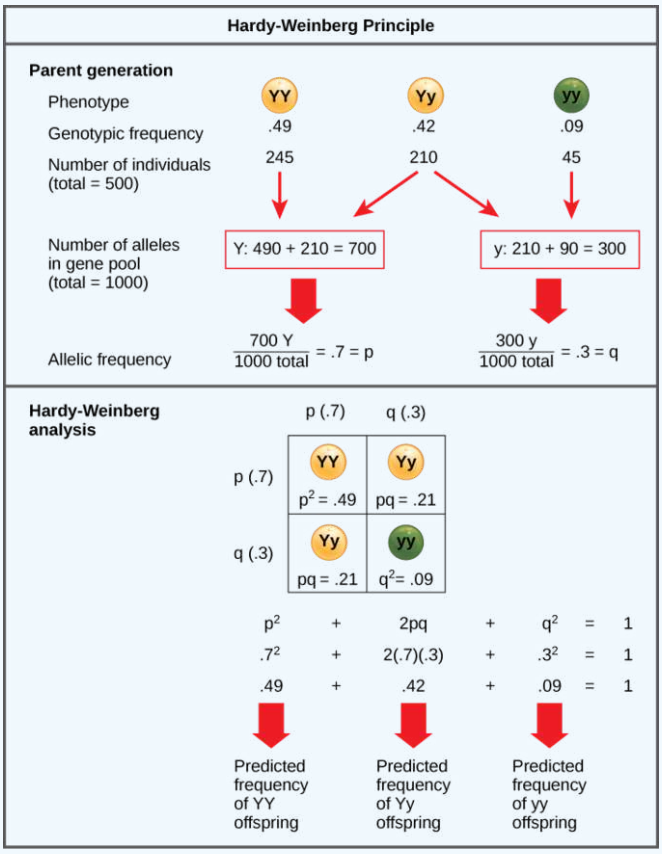


Figure 6.5.4: Predicted frequencies of alleles and genotypes of population with 9% green peas.

? Optional Exercies 6.5.2

In plants, violet flower color (V) is dominant over white (v). If q = 0.2 in a population of 500 plants, how many individuals would you expect to be homozygous dominant (VV), heterozygous (Vv), and homozygous recessive (vv)? How many plants would you expect to have violet flowers, and how many would have white flowers?

Answer

Remember that p indicates the frequency of the dominant allele (V) and q indicates the frequency of the recessive allele (v). It is easier to begin with the recessive allele.

In this population, if q = 0.2, then $q^2 = 0.04$. We know that q^2 is the frequency of homozygous recessive individuals, so 0.04 x 500 total plants (the overall population) = 20. Therefore, 20 plants would be expected to be homozygous recessive (white).

For the dominant allele, p, we need to use the formula p + q = 1. Since q = 0.2, we can calculate p + 0.2 = 1. From there, we get p = 1 - 0.2 so p = 0.8.

If p = 0.8, then p2 = 0.64. We know that p2 is the frequency of homozygous dominant individuals, so 0.64 x 500 total plants (the overall population) = 320. Therefore, 320 plants are expected to be homozygous dominant (violet).

To complete the problem, we calculate 2pq, or the frequency of heterozygous individuals. So, 2 x 0.8 x 0.2 = 0.32. We will then take and calculate 0.32 x 500 to get 160. Therefore, 160 plants are expected to be heterozygous (violet).

Optional Resource

Find an additional Hardy-Weinberg problem to solve, with solution and walk-through, here.

When the Hardy-Weinberg Law Fails

To see what forces lead to evolutionary change, we must examine the circumstances in which the Hardy-Weinberg law may fail to apply. In any of these cases (which is the reality of the natural world), evolution is occurring. There are five:

1. Mutation

The frequency of gene B and its allele b will not remain in Hardy-Weinberg equilibrium if the rate of mutation of B -> b (or vice versa) changes, or if a new allele B^o comes to be. By itself, this type of mutation probably plays only a minor role in evolution; the rates are simply too low. However, gene (and whole genome) duplication - a form of mutation - probably has played a major role in evolution. In any case, evolution depends on mutations because this is the only way that new alleles are created. After being shuffled in various combinations with the rest of the gene pool, these provide the raw material on which natural selection can act.

2. Gene Flow

Many species are made up of local populations whose members tend to breed within the group. Each local population can develop a gene pool distinct from that of other local populations. However, members of one population may breed with occasional immigrants from an adjacent population of the same species. This can introduce new genes or alter existing gene frequencies in the residents. Whether within a species or between species, gene flow increases the variability of the gene pool.

3. Genetic Drift

Genetic drift is evolution that happens when there is no selective advantage for the alleles that grow in frequency. That growth is due to chance events. For example, if a rock falls on a population of beetles that have green and red alleles and kills more of those individuals with the red allele, the gene frequency for this gene will change, but it was not adaptive. It just happened due to chance events. The smaller a population, the more susceptible it is to mechanisms such as genetic drift. Random events that alter allele frequencies will have a much larger effect when the gene pool is small.

If the population is small, Hardy-Weinberg may be violated. Chance, including abiotic impacts, alone may eliminate certain members out of proportion to their numbers in the population. In such cases, the frequency of an allele may begin to drift toward higher or lower values. Ultimately, the allele may represent 100% of the gene pool or, just as likely, disappear from it. Drift produces evolutionary change, but there is no guarantee that the new population will be more fit than the original one. Evolution by drift is aimless, not adaptive.

4. Nonrandom Mating

One of the cornerstones of the Hardy-Weinberg equilibrium is that mating in the population must be random. If individuals (usually females) are choosy in their selection of mates, the gene frequencies may become altered.

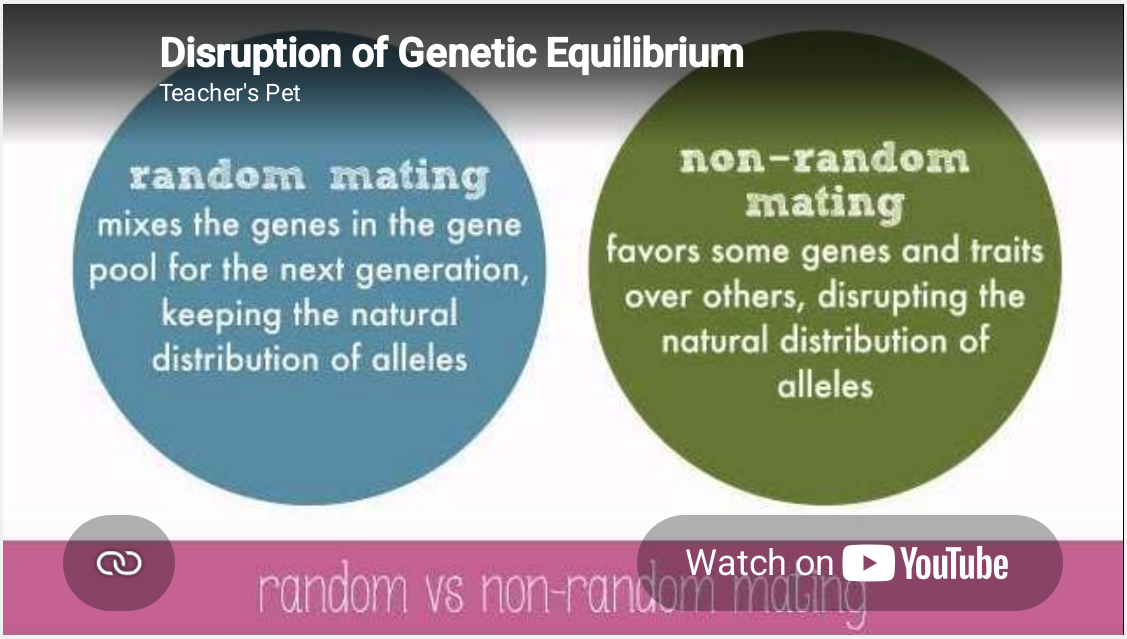
Nonrandom mating seems to be quite common. Breeding territories, courtship displays, "pecking orders" can all lead to it. In each case certain individuals do not get to make their proportionate contribution to the next generation. If some males reproduce more than others, then more of their genes are represented in the next generation.

5. Natural Selection

If individuals having certain genes are better able to produce mature offspring than those without them, the frequency of those genes will increase in the next generation. This is simply expressing Darwin's natural selection in terms of alterations in the gene pool. Natural selection results from *differential mortality* (some individuals survive longer than others) and/or *differential fecundity (some individuals have more offspring than others)*. Ultimately, this causes the sampling of one generation's gene pool to be

skewed; the next generation's gene pool is different from the first. Not every allele has an equal chance of being passed onto the next generation.

Video





This 4-minute video explains what the Hardy Weinberg equilibrium is and why finding a population that does not confirm to HW expectations tells you that the population is in the process of evolving with regards to one trait. Question after watching: The HW principle is defined using mathematical terms. Based on what you now know about the HW principle, what is being quantified and monitored in the HW principle to assess whether a population is evolving?

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CHAPTER OVERVIEW

Chapter 7: The History of Life, Systematics, and Phylogeny

Learning Objectives

- Discuss the need for a comprehensive classification system
- List the different levels of the taxonomic classification system
- Describe how systematics and taxonomy relate to phylogeny
- Discuss the components and purpose of a phylogenetic tree
- Compare homologous and analogous traits
- Discuss the purpose of cladistics
- Describe maximum parsimony
- Identify the web and ring models of phylogenetic relationships and describe how they differ from the original phylogenetic tree concept

7.1: Introduction

7.2: Deep Time

7.3: Origins of Life

7.4: Evidence for Early Life

7.5: Eukaryotic Origins

7.6: Systematics and Classification

7.7: Phylogeny and Cladistics

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7.1: Introduction

This bee and *Echinacea* flower could not look more different, yet they are related, as are all living organisms on Earth. By following pathways of similarities and changes—both visible and genetic—scientists seek to map the evolutionary past of how life developed from single-celled organisms to the tremendous collection of creatures that have germinated, crawled, floated, swam, flown, and walked on this planet.



Figure 7.1.1: The life of a bee is very different from the life of a flower, but the two organisms are related. Both are members the domain Eukarya and have cells containing many similar organelles, genes, and proteins. (credit: modification of work by John Beetham)

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- **20.0: Introduction** by OpenStax is licensed CC BY 4.0.

7.2: Deep Time

Deep Time

- Please read and watch the following Mandatory Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 1.5 hours.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Identify the major time frames on the geologic timeline
- Explain the evidence scientists use to explain the age of the Earth and mass extinctions

Geologic Time

The **geological time scale** in Figure 7.2.1 is one of the crowning achievements of science in general and geology in particular. It is a reference and communication system for comparing rocks and fossils found throughout the world and is geology's equivalent of the periodic table of the elements. It is also an important way to help organize when important milestones in the history of life on Earth occurred. For example, a paleontologist can call her colleague and say, "I just found an amazing new trilobite from the Devonian of British Columbia" and her colleague will immediately understand when in geological time that trilobite lived.

Most of the boundaries on the geological time scale correspond to the origination or extinction of particular fossils. Knowing when major groups of fossils first appeared or went extinct is therefore useful for determining the ages of rocks in the field. For example, if someone finds a rock with a trilobite fossil upon it, they will immediately know that the rock is Paleozoic in age, from 541 million years ago (Ma) to 252 Ma, and not older or younger; knowing the species of trilobite allows even greater precision.

The geological time scale provides a global summary of countless small-scale temporal correlations of rock layers made at local and regional scales. It is based almost entirely upon careful observations of the distributions of fossils in time and space.

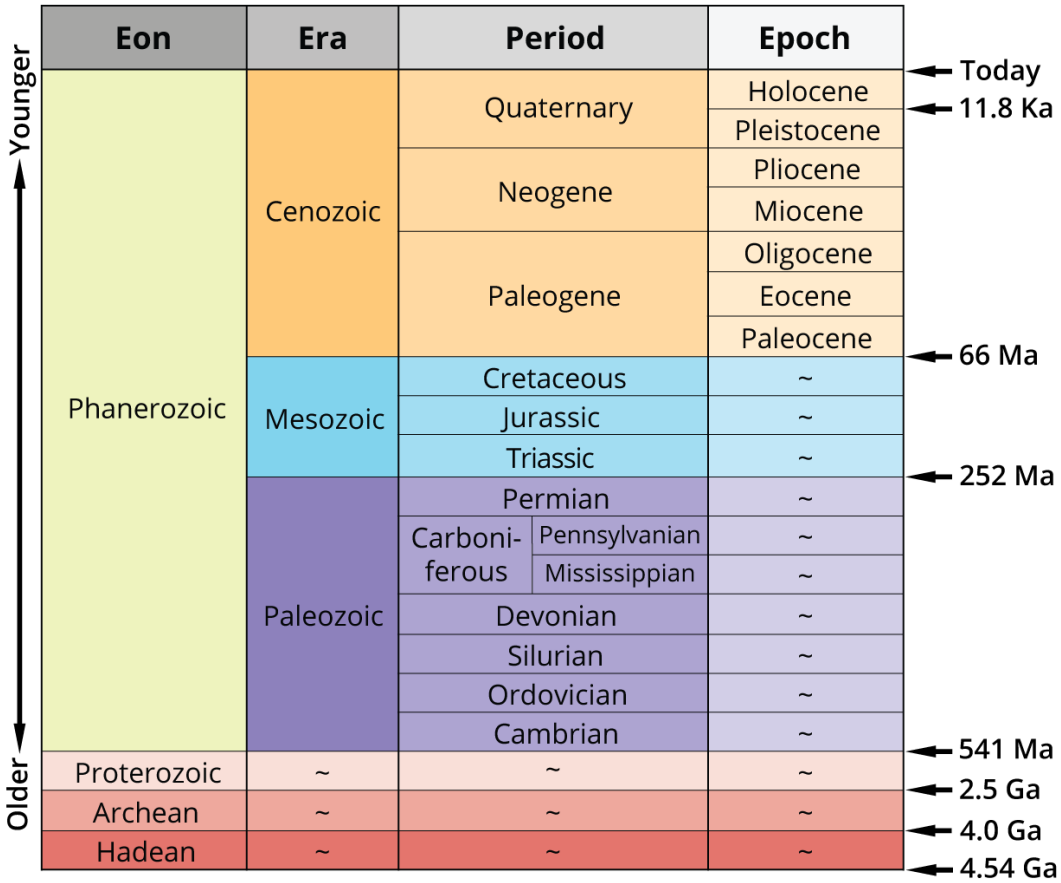


Figure 7.2.1: The geological time scale. Ka = thousands of years, Ma = millions of years, and Ga = billions of years. (Jonathan R. Hendricks CC-BY-SA 4.0)

Eons

The **eon** is the broadest category of geological time. All geologic time is measured in years before the present and are indicated in abbreviated terms: "Ga" indicates billions of years, "Ma" indicates millions of years and, "Ka" indicates thousands of years. The Earth is 4.54 billion years old (4.54 Ga). Earth's history is characterized by four eons; in order from oldest to youngest, these are the Hadeon, Archean, Proterozoic, and Phanerozoic. Collectively, the Hadean, Archean, and Proterozoic are sometimes informally referred to as the "**Precambrian**". (The Cambrian period defines the beginning of the Phanerozoic eon; so, all rocks older than the Cambrian are *Pre*cambrian in age.)

Humans live during the **Phanerozoic**, which means "visible life". This is the interval of geological time characterized by abundant, complex fossilized remains. Being the youngest eon of time, it is also well represented by rocks at Earth's surface. Because of these two factors, most paleontologists and geologists study fossils and rocks from the Phanerozoic eon. The Phanerozoic eon began 541 Ma (or, 0.541 Ga). Thus, the Phanerozoic eon represents only 12% of Earth's history.

Most of Earth's history is represented by the three Precambrian eons. These older eons tell the story of Earth's beginning, life's origin, and the rise of complex life. The Hadean and Archean are difficult eons to study, however, because they are exposed in very limited places on Earth's surface. Since they are the oldest eons, rocks that are Hadean and Archean in age are often buried far below younger rocks at the Earth's surface. Proterozoic rocks, which span nearly 2 billion years or 42% of Earth's history, are much more accessible. But, until recently, these have received significantly less attention from paleontologists than rocks from the younger, fossil-rich Phanerozoic eon. That is slowly beginning to change, however, as more clues about the origins of complex life begin to be revealed from Proterozoic-aged rocks.

Eras

Eons of geological time are subdivided into **eras**, which are the second-longest units of geological time. The Phanerozoic eon is divided into three eras: the Paleozoic, Mesozoic, and Cenozoic.

Most of our knowledge of the fossil record comes from the three eras of the Phanerozoic eon. The Paleozoic ("old life") era is characterized by trilobites, the first four-limbed vertebrates, and the origin of land plants. The Mesozoic ("middle life") era represents the "age of dinosaurs," though is also noteworthy for the first appearances of mammals and flowering plants. Finally, the Cenozoic ("new life") era is sometimes called the "age of mammals" and is the era we live in today.

As temporal points of reference, it is worth memorizing the ages of the boundaries that separate the three eras of the Phanerozoic eon. Long before geologists knew these absolute age dates, they realized that the boundaries represent important events in the history of life: **mass extinctions**. For example, many fossils that are commonly found in the youngest Paleozoic rocks are not found in overlying Mesozoic rocks. Similarly, dinosaur fossils found in the youngest Mesozoic rocks are never again found in the overlying Cenozoic rocks. Mass extinctions are when large numbers of species go extinct within a very short period of geologic time. Paleontologists and geologists used these mass extinction events to define these (and other) boundaries within the Phanerozoic portion of the geological time scale. It is therefore no coincidence that some of the major boundaries coincide with mass extinction events.

The older Archean and Proterozoic eons are similarly divided into several eras. For example, the youngest era of the Proterozoic eon is called the Neoproterozoic. For the sake of simplicity, these older eras are not included on the time scale shown at the top of this page; they do, however, exist.

Periods

Just as eons are subdivided into eras, eras are subdivided into units of time called **periods**. The most well-known of all geological periods is the Jurassic period of the Mesozoic era. The Paleozoic era is divided into six periods. From oldest to youngest, these are the Cambrian, Ordovician, Silurian, Devonian, Carboniferous, and Permian. Note that in the North America, the Carboniferous is divided into two separate periods: the Mississippian and the Pennsylvanian. The Mesozoic era is divided into the Triassic, Jurassic, and Cretaceous periods. Finally, the Cenozoic era is divided into three periods: the Paleogene, Neogene, and Quaternary.

Epochs and Ages

Periods of geological time are subdivided into **epochs**. In turn, epochs are divided into even narrower units of time called **ages**. For the sake of simplicity, only the epochs of the Paleogene, Neogene, and Quaternary periods are shown on the time scale at the top of this page. It is important to note, however, that all of the periods of the Phanerozoic era are subdivided into epochs and ages.

The Paleogene period is divided into--from oldest to youngest--the Paleocene, Eocene, and Oligocene epochs. The Neogene is divided into the Miocene and Pliocene epochs. Finally, the Quaternary is divided into the Pleistocene and Holocene epochs.

Some geologists think now that humans are having such a notable impact on the Earth and its life, a new, youngest epoch should be added to the Quaternary: the **Anthropocene**. These impacts include the destruction of large swaths of habitat, overexploitation of species, and planetary climate change, among others. These are discussed more in Unit 5. There is still considerable discussion in the geological community about whether this epoch should be added, as well as debate about what characteristics should define its beginning.

Video



This 12-minute video details the geologic record and important events through Earth's history that have shaped life. Question after watching: For each of the eras, eons, epochs, and periods in Figure 7.2.1, what is a main characteristic of this time period? Create a concept map, flow chart, table, or annotation of Figure 7.2.1.

Video



The first era of the current eon, the Paleozoic Era, is probably the most deceptively fascinating time in Earth's history. This 11-minute video describes it and the conditions of the Permian Extinction.

Question after watching:

Why do scientists say that mass extinctions provide opportunities? Continue to work on the notes that you started with the video above that outlines the major characteristics of each time period.

The Geologic and Evolutionary Record

A remarkable feature of Earth's history is how often evolutionary changes coincided with geologic and climatologic changes. In addition, consider that changes in geology (e.g., mountain formation or lowering of the sea level) can cause changes in climate. Changes in climate, in turn, can cause changes in geology through things like global loss/gain of ice. Geology and climate alter the habitats available for life. Past and present climate change will be covered in depth in Unit 5.

Here, we look at two types of geologic change that have had dramatic effects on life: **continental drift** and the impact of meteors**.**

Theory of Continental Drift

A body of evidence, both geological and biological, supports the conclusion that 200 million years ago, at the start of the Mesozoic era, all the continents were attached to one another in a single landmass, named **Pangaea**, seen in Figure 7.2.2. This drawing of

Pangaea is based on a computer-generated fit of the continents as they would look if the sea level were lowered by 1800 meters.

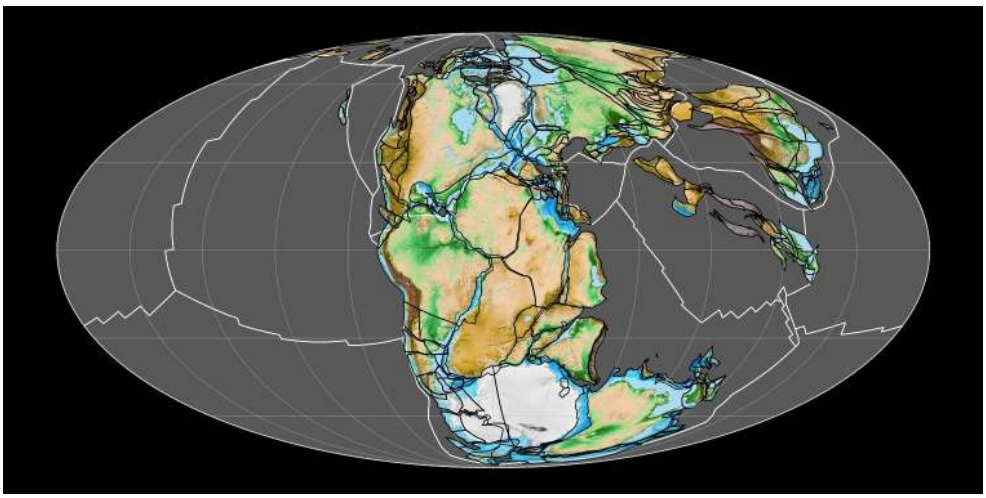


Figure 7.2.2: The supercontinent Pangaea in the early Mesozoic (at 200 Ma). The modern continents are highlighted for reference with North America in the upper left-hand corner, South America directly to the south, and Africa to the east. Antarctica is at the bottom with Australia to its right. (Fama Clamosa; CC-BY-SA 4.0)

During the Triassic Period, Pangaea began breaking up, first into two major landmasses:

- **Laurasia** in the Northern Hemisphere
- **Gondwana** in the Southern Hemisphere.

The present continents separated at intervals throughout the Mesozoic and Cenozoic Eras, eventually reaching the positions they have today. Evidence for this theory includes the shape of the continents, the geologic record, and fossils.

Shape of the Continents

The shape of the east coast of South America and the west coast of Africa and are strikingly complementary like puzzle pieces that fit together (Figure 7.2.2). This is even more dramatic when one fits the continents together using the boundaries of the continental slopes, (e.g., 1800 meters down), rather than the present-day shorelines.

Geology

- In both mineral content and age, the rocks in a region on the east coast of Brazil match precisely those found in Ghana on the west coast of Africa.
- The low mountain ranges and rock types in eastern Canada and the New England region of the United States appear to be continued in parts of Great Britain, France, and Scandinavia.
- India and the southern part of Africa both show evidence of periodic glaciation during Paleozoic times (even though both are now close to the equator). The pattern of glacial deposits in the two regions match each other and glacial deposits found in South America, Australia, and Antarctica.

Fossils

- Fossil reptile species found in South Africa are also found in Brazil and Argentina.
- Fossil amphibians and reptiles found in Antarctica are also found in South Africa, India, and China.
- Most of the marsupials alive today are confined to South America and Australia. If these two continents were connected by Antarctica in the Mesozoic, as the theory suggests, one might expect to find fossil marsupials there. In March 1982, this prediction was fulfilled with the discovery in Antarctica of the remains of *Polydolops*, a 2.7 meter marsupial.

Video



This 9-minute video discusses supercontinents and how their formation and breakup shaped life. Question after watching: What type of fossils might you expect to find in Kenorland? Why (what is the rationale?) What about Rodinia? What kinds of fossils might be found in Labrador?

Meteors: The Impact Hypotheses

The Cretaceous period, the last period of the Mesozoic, marked the end of the Age of Reptiles. It was followed by the Cenozoic era, the Age of Mammals. Although extinctions have occurred throughout the history of life, many of them occurred in a relatively brief period at the end of the Cretaceous. Why?

The Alvarez Hypothesis

In the 1980s, Louis Alvarez, his son Walter, and their colleagues proposed that a giant asteroid or comet striking the Earth some 66 million years ago caused the massive die-off at the end of the Cretaceous Period. The impact is hypothesized to have generated so much dust and gases that skies were darkened all over the Earth, photosynthesis declined, and global temperatures dropped. As many as 75% of all species, including most dinosaurs, became extinct.

The key piece of evidence for the Alvarez Hypothesis was the finding of thin deposits of clay containing the element iridium at the interface between the rocks of the Cretaceous and those of the Paleogene Epoch (called the K-Pg boundary after the German word for Cretaceous). Iridium is a rare element on Earth but occurs in certain meteorites at concentrations thousands of times greater than in the Earth's crust.

In the 1990s, the Alvarez Hypothesis gained strong support from the discovery of the remains of a huge (180 km in diameter) crater in the Yucatan Peninsula of Mexico that dated to 65 million years ago.

The abundance of sulfate-containing rock in the region suggests that the impact generated enormous amounts of sulfur dioxide (SO_2), which later returned to Earth as long-lasting showers of acid rain. A smaller crater in Iowa, formed at the same time, indicates another impact may have contributed to the devastation. Perhaps during this period, the Earth passed through the tail of a comet, or a swarm of asteroids. These repeated impacts would have made the Earth uninhabitable for many creatures of the Mesozoic Era.

Video





This entertaining video provides an overview of the evidence that led researchers to conclude that an asteroid impact caused the demise of the dinosaurs.

Question after watching:

One researcher, in tongue-in-cheek fashion, claims that we still live in the age of the dinosaurs. How do you think that the ages are named (i.e., why is this called the age of the mammals)? Dinosaurs are often thought to be ectotherms ("cold-blooded") like reptiles. However, birds are endothermic ("warm-blooded"). Based on this observation, do you think that dinosaurs were ectothermic or endothermic? Explain your reasoning.

Other Impacts

Mass extinctions have occurred at other times in Earth's history. There was another large extinction of non-dinosaur reptiles that occurred earlier, at the end of the Triassic. It was followed by a great expansion in the diversity of dinosaurs. The recent discovery of a layer enriched in iridium in rocks formed at the boundary between the Triassic and Jurassic suggests that impact from an asteroid or comet may have been responsible then, just as it was at the K-Pg boundary.

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Origins of Life

- Please read and watch the following Mandatory Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 1 hour.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Explain the different problems to solve, and scientific hypotheses, on the origins of life

The Origins of Life - A Mystery to Solve

To account for the origin of life on our Earth requires solving several problems:

1. How did the organic molecules that define life, e.g., amino acids, nucleotides, originate?
2. How were macromolecules assembled, e.g., proteins and nucleic acids, - a process requiring catalysts?
3. How were macromolecules able to reproduce themselves?
4. How were these macromolecules assembled into a system separate from their surroundings (i.e., a cell)?

Several hypotheses address each of these problems.

Video





This 13-minute video provides an overview of the origins of life, exploring along the way "what is life"? Question after watching: "Life is what living things do" (in contrast to what living things have). What does this mean? Do you agree with this statement based on what you know so far from this course?

Problem 1: How did the organic molecules that define life, e.g., amino acids, nucleotides, originate?

For the first problem, four hypotheses have been proposed:

- Hypothesis 1: Organic molecules were synthesized from inorganic compounds in the atmosphere,
- Hypothesis 2: Organic molecules rained down on the Earth from outer space,
- Hypothesis 3: Organic molecules were synthesized at hydrothermal vents on the ocean floor, and/or
- Hypothesis 4: Organic molecules were synthesized when comets or asteroids struck the early Earth.

Hypothesis 1: Organic molecules were synthesized from inorganic compounds in the atmosphere

In the fall of 1951, Stanley Miller was a graduate student looking for a research project. He attended a lecture by Nobel Laureate Harold C. Urey. Urey described how the earth's atmosphere was thought to be in its early formation and how it might have led, through chemical reactions, to the formation of the first organic molecules. Miller decided to test this idea. He created an apparatus that mimicked the earth's early conditions and atmosphere (or at least, what was thought, in 1951, to be the earth's early

conditions). The apparatus is shown in Figure 7.3.1. He filled it with water (H2O), methane (CH4), ammonia (NH3), and hydrogen (H2) but no oxygen since before life existed no oxygen had been released in the atmosphere by photosynthesis. The mixture circulated in the system by continuously boiling and then condensing/cooling the water. The gases passed through a chamber containing two electrodes with a spark passing between them, simulating lightening.

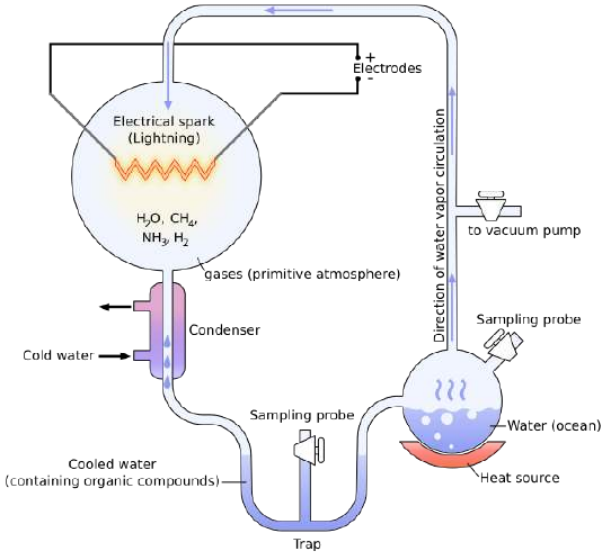


Figure 7.3.1: Miller experiment. (CC BY-SA; Yassine Mrabet).

At the end of the week-long experiment, Miller used paper chromatography to analyze the chemicals found in the flask. He discovered it now contained several amino acids (glycine, alanine, and aspartic acid) as well as other organic molecules, such as gamma-amino butyric acid or GABA (a chemical now used by many animals as a neurotransmitter).

It is now thought that the atmosphere of the early Earth was different than Miller supposed. However, in the years since Miller's work, many variants of his procedure have been tried with different mixtures of gases as our understanding of the early Earth's composition has changed. In nearly all versions of the experiment, organic molecules have almost always been formed, including the following results:

- 17 of the 20 amino acids used in protein synthesis, and all the purines and pyrimidines used in nucleic acid synthesis can be created in experiments similar to Miller's. They are easy to create by chemical reactions outside of living organisms.
- The synthesis of ribose, and thus of nucleotides, has been much more difficult outside of living organisms. However, success in synthesizing pyrimidine ribonucleotides under conditions that might have existed in the early Earth was reported in the 14 May 2009 issue of the scientific journal Nature. Thus, the synthesis of these molecules outside of a living organism is possible.
- In 2015, chemists in Cambridge, England led by John Sutherland reported that they had synthesized precursors for 12 of the 20 amino acids used in protein synthesis, two (of the four) ribonucleotides used to make RNA, and a precursor of lipids - all from a non-living system. In fact, they created these molecules using only hydrogen cyanide (HCN) and hydrogen sulfide (H_2S) irradiated with ultraviolet light in the presence of mineral catalysts.

Hypothesis 2: Organic molecules rained down on the Earth from outer space

Video





This 4 min video provides an overview of the hypothesis that the molecules of life may have been brought to earth from outer space.

Question after watching: What is the evidence for the hypothesis of Panspermia?

Astronomers, using infrared spectroscopy, have identified a variety of organic molecules in interstellar gas clouds, including methane (CH_4), methanol (CH_3OH), formaldehyde (HCHO), cyanoacetylene (HC_3N) (which in Miller-type experiments is a precursor to the pyrimidine cytosine), polycyclic aromatic hydrocarbons (PAHs), as well as other important molecules such as carbon dioxide (CO_2), carbon monoxide (CO), ammonia (NH_3), hydrogen sulfide (H_2S), and hydrogen cyanide (HCN). There are organic molecules in space. These could have found their way to earth and provided the building blocks of life.

Several laboratories have reported producing amino acids and other organic molecules by taking a mixture of molecules known to be present in interstellar space such as ammonia (NH_3), carbon monoxide (CO), methanol (CH_3OH), water (H_2O), and hydrogen cyanide (HCN) and exposing it to temperatures close to that of space (near absolute zero) and intense ultraviolet (UV) radiation. In other words, there is nothing special about creating organic molecules – they arise in the universe through the conditions found in space. They do not require living systems to create them. Whether or not the molecules that formed terrestrial life arrived here from space, there is little doubt that organic matter continuously rains down on the Earth (estimated at 30 tons per day). These could have served as the building blocks for the first living organism.

Alternatively, organic molecules can be transported to Earth via meteorites as demonstrated by the Murchison Meteorite that fell near Murchison, Australia on 28 September 1969 (Figure 7.3.2). This meteorite contains many organic molecules including purines and pyrimidines and 12 different amino acids. The relative proportion of each amino acid in the meteorite mirrored those found as a result of Miller's experiments. This suggests that abiotic chemical reactions produce these organic molecules easily and reliably, and whether they were formed on the early earth or is space, they could have served to construct the first living organism.

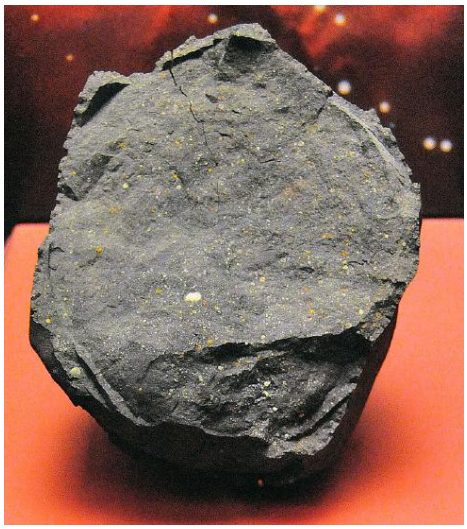
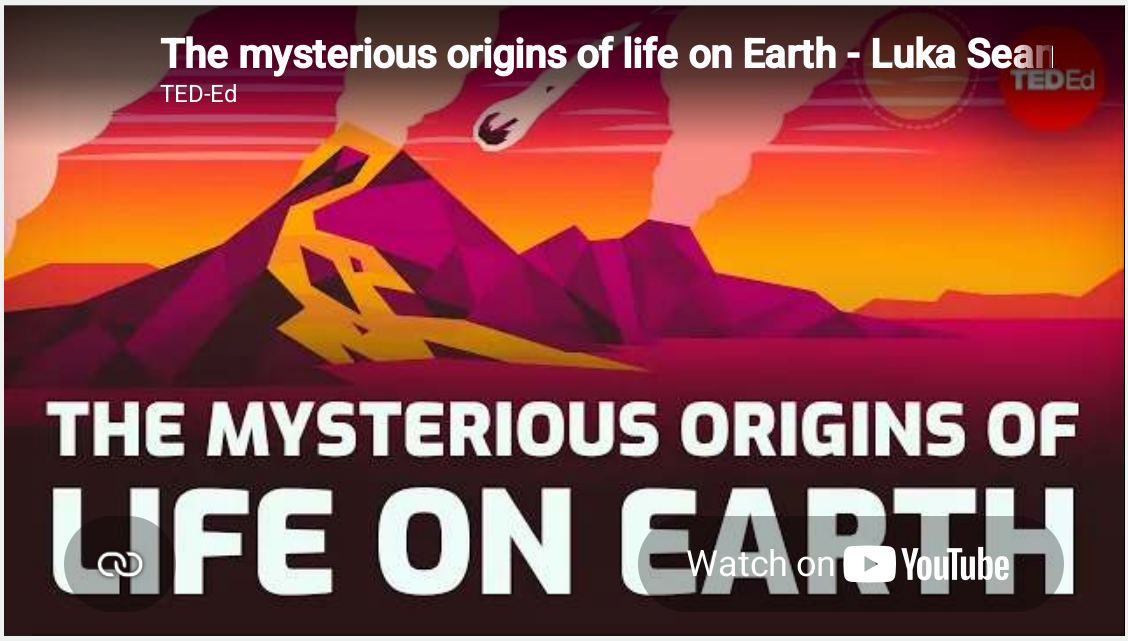


Figure 7.3.2: Murchison meteorite at The National Museum of Natural History (Washington). (CC SA-BY 3.0; Basilicofresco)

Hypothesis 3: Organic molecules were synthesized at hydrothermal vents on the ocean floor

Another location suspected of serving as a cradle for life are deep-sea hydrothermal vents. These vents would have provided a relatively stable environment for life to begin while the early planet was bombarded by meteorites. Some deep-sea hydrothermal vents discharge copious amounts of hydrogen, hydrogen sulfide, and carbon dioxide at temperatures around 100°C. The gases bubble up through chambers rich in iron sulfides (FeS, FeS_2). The iron sulfide surfaces can facilitate chemical reactions (i.e., serve as catalysts) that lead to the formation of simple organic molecules like acetate. Note also that life today depends on enzymes that have Fe and S atoms in their active (catalytic) site, so these iron sulfide minerals could have been a precursor for today's living system enzymes.

Video





This 5-minute video provides an overview of the hypothesis that life began at hydrothermal vents.
Question after watching: What are some characteristics of LUCA? How do we know that this organism had these characteristics?

Hypothesis 4: Organic molecules were synthesized when comets or asteroids struck the early Earth

The ingredients for the creation of organic molecules include basic inorganic chemicals like carbon dioxide (CO_2) or hydrogen cyanide (HCN), but the rearrangement of their atoms into organic molecules also requires an infusion of energy. In the hypotheses we have investigated thus far, the energy came from lighting, chemical gradients, or UV light. In this hypothesis, the energy comes from the impact of meteorites with the early Earth.

Researchers in the Czech Republic reported in 2014 that they had succeeded in the abiotic synthesis of adenine (A), guanine (G), cytosine (C), and uracil (U) — the four bases found in RNA and three of the four found in DNA. They achieved this by bombarding a mixture of formamide and clay with powerful laser pulses that mimicked the temperature and pressure expected when a large meteorite strikes the Earth. Formamide is a simple substance, CH_3NO, thought to have been abundant on the early Earth and containing the four elements fundamental to all life. It could serve as a basis for the creation of many of the organic molecules used by living systems today. Thus, the meteorite impact may have sparked life on earth.

Problem 2: How were macromolecules assembled?

Once the organic molecules of life are created (monomers), the next step in the creation of life is to assemble them into large macromolecules (polymers). For example, nucleotides need to be assembled into RNA or DNA; and amino acids need to assemble into proteins.

Researchers who study this problem think that early polymers were assembled on solid, mineral surfaces These surfaces worked like catalysts, holding the monomers in the right orientation to facilitate their assembly into larger polymers, and once formed the mineral surface held on to the polymer and in so doing, protected them from degradation. In the laboratory, polypeptides and polynucleotides (RNA molecules) containing about ~50 monomers linked together have been synthesized on mineral (e.g., clay) surfaces.

Today, all living organisms have metabolism to create more of themselves from simpler building blocks and this activity depends on enzymes. Until recently, every enzyme science knew off was a protein. But proteins are synthesized from information encoded in DNA and translated into mRNA. So here is a chicken-and-egg dilemma. The synthesis of DNA and RNA requires proteins. So proteins cannot be made without nucleic acids and nucleic acids cannot be made without proteins.

The discovery that certain RNA molecules have enzymatic activity on their own provides a possible solution. These RNA molecules, called **ribozymes**, incorporate both the features required of life: storage of information and the ability to act as catalysts. This leads to what is known as the **RNA World Hypothesis**.

Video



This 3-minute video describes the RNA World Hypothesis.

Question after watching: In your notes, write a short description of the RNA world hypothesis and the argument for it. How could natural selection operate on the molecular level (as demonstrated in the RNA World Hypothesis)?

While no ribozyme in nature has yet been found that can replicate itself, ribozymes have been synthesized in the laboratory (using artificial selection) that can catalyze the assembly of short oligonucleotides into exact complements of themselves. The ribozyme serves as both the *template* on which short lengths of RNA ("oligonucleotides" are assembled following the rules of base pairing and the *catalyst* for covalently linking these oligonucleotides.

In principle, life might have begun as a self-replicating RNA. Only later did proteins take over the catalytic machinery of metabolism and DNA take over as the repository of the genetic code. Several other bits of evidence support the RNA World Hypothesis:

- Many of the enzyme cofactors important for life today are based on a ribose nucleotide; for example:
  - ATP
  - NAD
  - FAD
  - coenzyme A
  - cyclic AMP

    - GTP
- In the cell, all deoxyribonucleotides are synthesized from ribonucleotide precursors.
- Many organisms control the transcription and/or translation of certain genes with RNA molecules, not protein molecules.

Problem 3: How were macromolecules able to reproduce themselves?

Once macromolecules were created, the next problem we must try to understand is how they were able to generate more of themselves, identical in composition and structure. Without this reproductive ability, life would change each generation and there would be no continuity.

The advantage of the RNA World Hypothesis is that it proposes a way in which the creation of the first macromolecule (an RNA with the ability to encode information and replicate itself) and of creating progeny with similar properties. It would explain this step, and provide a mechanism for natural selection to work on this population of "organisms" (RNA ribozymes) to change, with the best replicators emerging from the pool in greater number at each succeeding generation.

For the other hypotheses about the creation of life, the mechanism for the reproduction of macromolecules is less understood.

Problem 4: How were these macromolecules assembled into a system separate from their surroundings (i.e., a cell)?

To function, the machinery of life must be separated from its surroundings so that the building blocks are held in greater concentration to facilitate chemical reactions and so that the products do not float away. The chemicals of life need to be separated from the extracellular fluid (ECF). Today, this function is provided by the plasma membrane.

The plasma membranes of all current living organisms are made of a double layer of phospholipids. They are only permeable to small, uncharged molecules like H_2O, CO_2, and O_2. Specialized transmembrane transporters are needed for ions, hydrophilic, and charged organic molecules (e.g., amino acids and nucleotides) to pass into and out of the cell.

One of the key researchers in this field, Jack Szostak and colleagues from Harvard University, has confirmed that fatty acids, fatty alcohols, and monoglycerides, all molecules that can be synthesized under prebiotic conditions, can also form lipid bilayers and these can spontaneously assemble into enclosed vesicles.

Unlike phospholipid vesicles, these

- admit charged molecules like nucleotides
- admit hydrophilic molecules like ribose
- grow by self-assembly
- are impermeable to, and thus retain, polymers like oligonucleotides.

Here, then, is a simple system that is a plausible model for the creation of the first cells from the primeval "soup" of organic molecules.

Other hypotheses have been proposed, like the formation of an iron sulfide cell as a precursor of cells in deep-sea hydrothermal vents. The advantage of these enclosures is that they would have served as catalysts as well as to keep the chemicals created by the early life from floating away. In time, lipids may have come to coat the surface of these metal cells and bud away, seeding life in the ocean.

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7.4: Evidence for Early Life

Evidence for Early Life

- Please read and watch the following Mandatory Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 1 hour.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
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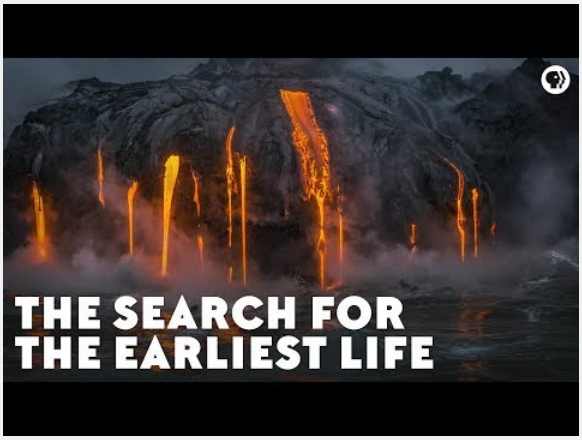
Learning Objectives

- Discuss the origins of prokaryotic organisms in terms of the geologic timeline
- Distinguish Bacteria from Archaea in terms of their origins
- Discuss the distinguishing features of extremophiles and the environments that produce biofilms

Prokaryotes, the First Inhabitants of Earth

Video





This 5.5-minute video describes the search for the earliest evidence of life on earth.
Question after watching: Evidence for life on earth is that it happened relatively quickly after the formation of the planet. What are the implications of this hypothesis?

When and where did life begin? What were the conditions on earth when life began? **Prokaryotes** were the first forms of life on earth, existing for billions of years before plants and animals appeared. The earth and its moon are about 4.54 Ga. This estimate is based on evidence from radiometric dating of meteorite material together with other substrate material from the Earth and the moon.

Early earth had a very different atmosphere than it does today, for example, it contained less molecular oxygen since photosynthesis had not yet evolved to produce it as a by-product. It was also subjected to strong radiation from outer space since the composition of the early atmosphere did not protect the surface as it does today. Thus, the first organisms would have flourished where they were more protected, such as in ocean depths or beneath the surface of the earth. Also at this time, strong volcanic activity was common on Earth. It is probable that these first organisms, the first prokaryotes, were adapted to very high temperatures. The early earth was prone to geological upheaval, volcanic eruptions, and bombardment by mutagenic radiation from the sun. The first organisms were prokaryotes that could withstand these harsh conditions.

Although prokaryotic cell fossils date to almost 3.5 billion years ago, most prokaryotes do not have distinctive morphologies; fossil shapes cannot be used to distinguish them between Archaea and Bacteria. Instead, chemical fossils of unique lipids are more informative because such compounds do not occur in other organisms. Some publications suggest that archaean or eukaryotic lipid remains are present in rock formations dating from 2.7 billion years ago in Precambrian formations. The oldest such traces come from Greenland, in Earth's oldest sediments, which formed 3.8 billion years ago.

? Optional Activity 7.4.1

Why do scientists believe that the first organisms on Earth were extremophiles?

Answer

Because the environmental conditions on early Earth were extreme by current standards: high temperatures, lack of oxygen, high radiation, etc.

Current Model

The first, living organisms were likely prokaryotes, which may have evolved from one or more of the circumstances in Section 3.3.2. The evidence strongly suggests that eukaryotes evolved much later in the history of life. They are discussed in Section 3.3.4.

Evolution of Prokaryotes

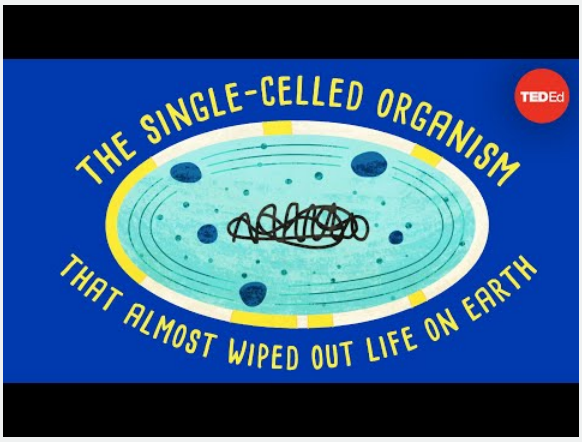
In the recent past, scientists grouped living things into five kingdoms (animals, plants, fungi, protists, and prokaryotes) based on several criteria such as: the absence or presence of a nucleus and other membrane-bound organelles, the absence or presence of cell walls, multicellularity, etc. In the late 20th century, the pioneering work of Carl Woese and others compared sequences of the small-subunit ribosomal RNA (SSU rRNA), which are found in every living organism. This resulted in insights into the evolution of living organisms, their relationships, and a more fundamental way to group organisms on earth. Based on differences in the structure of cell membranes and in the sequences of their rRNA, Woese and his colleagues proposed that all life on earth evolved along three domains. The **Domain Bacteria** comprises all eubacteria (a type of prokaryote), the **Domain Archaea** comprises the archaeans (also a type of prokaryote), and the **Domain Eukarya** comprises all eukaryotes, including organisms in the kingdoms Animalia, Plantae, Fungi, and Protista.

Two of the three domains, Bacteria and Archaea, are prokaryotic. Based on fossil and molecular evidence, prokaryotes were the first inhabitants on Earth, appearing 3.5-3.8 Ga during the Precambrian Period. These organisms are abundant and ubiquitous; that is, they are present everywhere on Earth today. In addition to inhabiting moderate environments, they are found in extreme conditions: from boiling hot springs to permanently frozen environments such as tundra and sea ice; from salty environments like the Dead Sea to environments under tremendous pressure, such as the depths of the ocean; and from areas without oxygen, such as a waste management plant, to radioactively-contaminated regions, such as Chernobyl in Ukraine. Prokaryotes reside in the human

digestive system and on human skin, are responsible for some illnesses, and serve an important role in the preparation of many foods.

Video





This 4-minute video explains how bacteria almost extinguished life on earth early in life's history. Question after watching: Why was the creation of oxygen by photosynthesis problematic?

Prokaryotic Life

Microbial Mats

Microbial mats**,** or large **biofilms**, may represent the earliest forms of life on earth; there is fossil evidence of their presence starting about 3.5 billion years ago. A microbial mat is a multi-layered sheet of prokaryotes that includes mostly bacteria, but also archaea (Figure 7.4.1). Microbial mats are a few centimeters thick, typically growing where different types of materials interface, mostly on moist surfaces. The different species of prokaryotes that comprise the mats use different metabolic pathways, which is the reason for their varied colors. Prokaryotes in a microbial mat are held together by a glue-like sticky substance that they secrete called **extracellular matrix**.

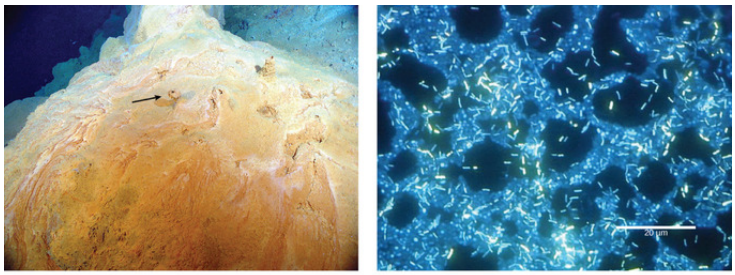


Figure 7.4.1: (a) This microbial mat, about one meter in diameter, grows over a hydrothermal vent in the Pacific Ocean in a region known as the "Pacific Ring of Fire." The mat helps retain microbial nutrients. Chimneys, such as the one indicated by the arrow, allow gases to escape. (b) In this micrograph, individual bacteria in a microbial mat are visualized using fluorescence microscopy.

The organisms in the first biofilms likely obtained their energy from chemicals found near **hydrothermal vents**. A hydrothermal vent is a fissure in the Earth's surface that releases geothermally-heated water as well as chemicals leached from rocks in the earth's interior. With the evolution of photosynthesis about 3 billion years ago, some prokaryotes in microbial mats came to use a more widely available energy source, sunlight, whereas others were still dependent on chemicals from hydrothermal vents for energy and food.

? Optional Activity 7.4.2

Microbial mats _____.

A. are the earliest forms of life on Earth
B. obtain their energy and food from hydrothermal vents
C. are multi-layered sheets of prokaryotes including mostly Bacteria but also Archaea
D. all of the above

Answer

D. All of the above

The Ecology of Biofilms

Until a couple of decades ago, microbiologists used to think of prokaryotes as isolated entities living apart. This model, however, does not reflect the now better-understood ecology of prokaryotes, most of which prefer to live in communities where they can interact. A biofilm is a microbial community held together in a gummy-textured matrix that consists primarily of polysaccharides secreted by the organisms, together with some proteins and nucleic acids (Figure 7.4.2). Biofilms grow attached to surfaces to secure them in place. Some of the best-studied biofilms are composed of prokaryotes, although fungal biofilms have also been described, as well as some composed of a mixture of fungi and bacteria.

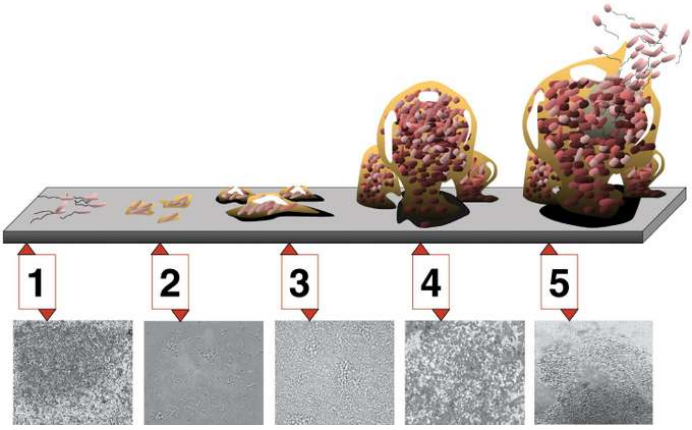


Figure 7.4.2: Micrographs of a *Pseudomonas aeruginosa* biofilm in each of the stages of development. Biofilm development occurs in five stages as shown. During stage 1, initial attachment, prokaryotes adhere to a solid surface. During stage 2, irreversible attachment, hairlike appendages called pili permanently anchor the prokaryotes to the surface. During stage 3, maturation I, the biofilm grows through cell division and recruitment of other prokaryotes. An extracellular matrix composed primarily of polysaccharides holds the biofilm together. During stage 4, maturation II, the biofilm continues to grow and takes on a more complex shape. During stage 5, dispersal, the biofilm matrix is partly broken down, allowing some prokaryotes to escape and colonize another surface.

Biofilms are present almost everywhere: they are visible on the surface of some lakes and can cause the clogging of pipes. They also colonize household surfaces, such as kitchen counters, cutting boards, sinks, and toilets, as well as places on the human body, such as the surfaces of our teeth (plaque). They also play a major role in food contamination.

Interactions among the organisms that populate a biofilm, together with their protective extracellular matrix, make these communities more robust than free-living prokaryotes. The sticky substance that holds bacteria together also excludes most antibiotics and disinfectants, making biofilm bacteria hardier than their free-living counterparts. Overall, biofilms are very difficult to destroy because they are resistant to many common forms of sterilization.

Stromatolites

Fossilized microbial mats represent the earliest record of life on earth. A **stromatolite** is a sedimentary structure formed when minerals are precipitated out of water by prokaryotes in a microbial mat (Figure 7.4.3). Stromatolites form layered rocks made of carbonate or silicate. Although most stromatolites are artifacts from the past, there are places on earth where stromatolites are still forming. For example, growing stromatolites have been found in the Anza-Borrego Desert State Park in San Diego County, California.



Figure 7.4.3: Stromatolites: (a) These living stromatolites are located in Shark Bay, Australia. (b) These fossilized stromatolites, found in Glacier National Park, Montana, are nearly 1.5 billion years old.

In addition, NASA is studying Pavilion Lake, north of Whistler BC, for its microbialites population (Figure 7.4.4). These bacteria colonies live at the bottom of the lake and precipitate minerals that form coral-like structures. These structures formed 10,000 years ago, when the glaciers retreated from the area.

Figure 7.4.4: Examples of microbialite morphologies in Pavillion Lake (CC-BY-SA; Schulze-Makuch, D. et al. https://www.mdpi.com/2075-1729/3/1/21#)

Video





This 2-minute video describes what stromatolites are.
Question after watching: Why are stromatolites relevant to the study of the origin and early evolution of life?

Microbes Are Adaptable: Life in Moderate and Extreme Environments

Some organisms have developed strategies that allow them to survive harsh conditions. Prokaryotes thrive in a vast array of environments; some grow in conditions that would seem very normal to us, whereas others are able to thrive and grow under conditions that would kill a plant or animal. Almost all prokaryotes have a cell wall: a protective structure that allows them to survive in both hyper- and hypo-osmotic conditions. Some soil bacteria can form endospores that resist heat and drought, thereby allowing the organism to survive until favorable conditions recur. These adaptations, along with others, have made bacteria the most abundant life form in all terrestrial and aquatic ecosystems today.

Other bacteria and archaea are adapted to grow under extreme conditions and are called **extremophiles**, meaning “lovers of extremes”. Extremophiles have been found in all kinds of environments: the depth of the oceans, hot springs, the Arctic and the Antarctic, in very dry places, deep inside the Earth, in harsh chemical environments, and in high radiation environments, just to mention a few (Figure 7.4.5).



Figure 7.4.5: Certain prokaryotes can live in extreme environments such as the Morning Glory pool, a hot spring in Yellowstone National Park, Wyoming, USA. The spring's vivid blue color is from prokaryotes that thrive in its hot waters.

These organisms give us a better understanding of prokaryotic diversity and help us understand the range of environmental conditions that life can tolerate. This allows us to understand where life may have originated, and where we may find it in the future (including on other planets and moons in the solar system). In addition, the unique enzymes and chemical pathways that extremophiles develop to adapt to their environment raise the possibility of finding new therapeutic drugs or industrial applications.

Because they have specialized adaptations that allow them to live in extreme conditions, many extremophiles cannot survive in moderate environments. There are many different groups of extremophiles. They are identified based on the conditions in which they grow best. For examples, organisms that live in acidic (low pH) conditions are called **acidophiles**. Those that live in hot environments are called **thermophiles**. Some habitats are extreme in multiple ways. For example, a soda lake is both salty and alkaline, so organisms that live in a soda lake must be both **alkaliphiles** and **halophiles**.

Other extremophiles, like radioresistant organisms, do not prefer an extreme environment (in this case, one with high levels of radiation), but have adapted to survive in it (Figure 7.4.6).

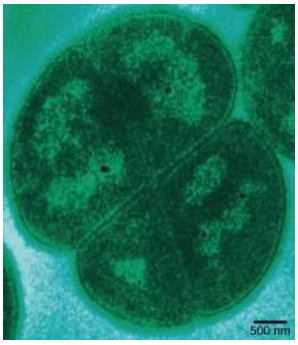


Figure 7.4.6: *Deinococcus radiodurans*, visualized in this false-color transmission electron micrograph, is a prokaryote that can tolerate very high doses of ionizing radiation. It has evolved DNA repair mechanisms, refined from existing ones found in other organisms, but specialized for its environment, that allow it to reconstruct its chromosome even if it has been broken into hundreds of pieces by radiation or heat.

Prokaryotes in the Dead Sea

One example of a harsh environment is the Dead Sea, a hypersaline basin that is located between Jordan and Israel. **Hypersaline** environments are concentrated seawater. In the Dead Sea, the sodium concentration is 10 times higher than that of seawater. The water also contains high levels of magnesium (about 40 times higher than seawater) that are toxic to most living things. Iron, calcium, and magnesium, elements that form divalent ions (Fe^{2+}, Ca^{2+}, and Mg^{2+}), produce what is commonly referred to as "hard" water. Taken together, the high concentration of divalent cations, the acidic pH (6.0), and the intense solar radiation flux make the Dead Sea a unique, and hostile, ecosystem.



Figure 7.4.6: (a) The Dead Sea is hypersaline. Nevertheless, salt-tolerant bacteria thrive in this sea. (b) These halobacteria cells can form salt-tolerant bacterial mats.

Career Connection: Paleontologist

Natural history museums display the fossil casts of extinct animals and information about how these animals evolved, lived, and died. Paleontologists are scientists who study past life. They use fossils to observe and explain how life evolved on Earth and how species interacted with each other and with the environment. A paleontologist must be knowledgeable in biology, ecology, chemistry, geology, and other scientific disciplines. A paleontologist's work may involve field studies: searching for and studying fossils. In addition to digging for and finding fossils, paleontologists also prepare fossils for further study and analysis. Although dinosaurs are probably the first animals that come to mind when thinking about paleontology, paleontologists study everything from plant life, fungi, and fish to sea animals and birds.

An undergraduate degree in earth science or biology is a good place to start toward the career path of becoming a paleontologist. Most often, a graduate degree is necessary. Additionally, work experience in a museum or in a paleontology lab is useful.

Optional Resource

Paleontology in Western Canada

In Western Canada, there are several sites rich in fossils that are active sites of research. The Burgess Shales, located in Yoho National Park in BC (near Golden) is a designated World Heritage Site. Fossils from this location date to 508 Ma, in the middle of the Cambrian Explosion, when many animal body plans first evolved. Although the site is now at the top of the Rockies, 508 Ma it was at the bottom of a shallow sea where a mudslide likely buried many animals, preserving the structure of even soft-bodied creatures.

In Alberta, Dinosaur Provincial Park is also a UNESCO World Heritage site. Located 48 km east of Calgary, it is not just a recreational area but also an active research site for dinosaurs that lived roughly 75 Ma in the late Cretaceous. Tyrannosaurus, one of the most well-known large dinosaurs, are found here. Dinosaur bones are so plentiful that they are regularly seen sticking out of the ground. Other active dig sites exist in Edmonton, Alberta's river valley and around Grande Prairie.

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7.5: Eukaryotic Origins

Eukaryotic Origins

- Please read and watch the following Mandatory Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 2 hours.
- Optional Activities are embedded.
- Bolded terms are located at the end of the unit in the Glossary. There is also a Unit Summary at the end of the Unit.
- To navigate to Unit 3.4, use the Contents menu at the top of the page OR the right arrow on the side of the page.
    - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- List the unifying characteristics of eukaryotes
- Describe what scientists know about the origins of eukaryotes based on the last common ancestor
- Explain endosymbiotic theory

Living things fall into three large groups: Archaea, Bacteria, and Eukarya. The first two have prokaryotic cells, and the third contains all eukaryotes. A relatively sparse fossil record is available to help discern what the first members of each of these lineages looked like, so it is possible that all the events that led to the last common ancestor of extant eukaryotes will remain unknown. However, the comparative biology of extant organisms and the limited fossil record provide some insight into the history of Eukarya.

The earliest fossils of living organisms appear to be Bacteria, most likely cyanobacteria. They are about 3.5 billion years old and are recognizable because of their relatively complex structure and, for prokaryotes, relatively large cells. Most other prokaryotes have small cells, 1 or 2 µm in size, and would be difficult to pick out as fossils. Most living eukaryotes have cells measuring 10 µm or greater. Structures this size, which might be fossils, appear in the geological record about 2.1 billion years ago.

Characteristics of Eukaryotes

Data from these fossils have led comparative biologists to the conclusion that living eukaryotes are all descendants of a single common ancestor. Mapping the characteristics found in all major groups of eukaryotes reveals that the following characteristics must have been present in the last common ancestor.

These characteristics that are common to nearly all eukaryotes include:

1. Cells with nuclei that are surrounded by a nuclear envelope with nuclear pores. This is the single characteristic that is both necessary and sufficient to define an organism as a eukaryote. All currently living eukaryotes have cells with nuclei.
2. Mitochondria. An organelle that processes glucose using oxygen to produce ATP. Some extant eukaryotes have very reduced remnants of mitochondria in their cells, whereas other members of their lineages have “typical” mitochondria.
3. A cytoskeleton containing the structural and motility components called actin microfilaments and microtubules. All extant eukaryotes have these cytoskeletal elements.
4. Flagella and cilia, organelles associated with cell motility. Some extant eukaryotes lack flagella and/or cilia, but there is molecular evidence that they are descended from ancestors that possessed them.
5. Chromosomes, each consisting of a linear DNA molecule coiled around basic (alkaline) proteins called histones. The few eukaryotes with chromosomes lacking histones clearly evolved from ancestors that had them based on information contained in their DNA.
6. Mitosis, which is a process of cellular division wherein replicated chromosomes are divided and separated into two new cells using elements of the cytoskeleton. Mitosis is universally present in eukaryotes.
7. Sexual reproduction and meiosis, a process of cell division and genetic recombination unique to eukaryotes.

Endosymbiosis and the Evolution of Eukaryotes

To understand eukaryotic organisms, it is necessary to understand that all **extant** (currently living) eukaryotes are descendants of an organism that was a composite of a host cell and the cell(s) of an alpha-proteobacterium that "took up residence" inside it. This major theme in the origin of eukaryotes is known as **endosymbiosis**, one cell engulfing another such that the engulfed cell survives and both cells benefit. Over many generations, a **symbiotic** relationship can result if the two organisms depend on each other so completely that neither could survive on its own. Endosymbiotic events likely contributed to the origin of the last common ancestor of today's eukaryotes and to later diversification in certain lineages of eukaryotes such as plants. Before explaining this further, it is necessary to consider metabolism in prokaryotes.

Prokaryotic Metabolism

Prokaryotes are much more metabolically diverse than eukaryotes. This makes sense when considering that the evolution of eukaryotes represents only one branch of the tree of life, and a relatively recent one at that.

Many important metabolic processes such as **nitrogen fixation**, are never found in eukaryotes. One that is not unique to eukaryotes (i.e., some prokaryotes can do it), but that is present in all eukaryotes is the process of **aerobic respiration** and it happens in the mitochondria. This suggests that the ability to respire came from a type of prokaryote that could do aerobic respiration; they eventually became the eukaryotic cell's mitochondria. This is discussed in more detail below.

The Problem with Oxygen

While today's atmosphere is about one-fifth molecular oxygen (O_2), geological evidence shows that the atmosphere originally lacked O_2. Without oxygen, aerobic respiration would not be possible, and prokaryotes would have relied on fermentation as a means of transforming the energy in their food into something that they use for their cells. At some point around 3.5 billion years ago, some prokaryotes began using energy from sunlight to power the formation of organic compounds. That is, they evolved the ability to **photosynthesize**. The group of Gram-negative bacteria that gave rise to cyanobacteria used water as the hydrogen source and released O_2 as a waste product. They used chemical gradients across their cell membrane to do it.

Eventually, the amount of photosynthetic oxygen built up in some environments to levels that were toxic to the organisms living at that time. Oxygen is reactive (it is a strong electron acceptor) and can damage many organic compounds. Metabolic processes evolved to protect organisms from oxygen. Aerobic respiration, one of these processes, utilized the newly available chemical, and its properties as an electron acceptor, to extract energy out of reduced chemicals (a reduced chemical is one that contains many electrons). As energy was extracted from these reduced chemicals, the cell captured the energy to make ATP, a chemical it could readily use to power its processes. This ability to use oxygen to process reduced chemicals (i.e., aerobic respiration) became widely present among prokaryotes, including in a group we now call alpha-proteobacteria (described below).

Organisms that did not evolve aerobic respiration continued to exist, but the were restricted to living in oxygen-free environments. Originally, oxygen-rich environments were likely localized around places where cyanobacteria were active. By about 2 billion years ago, however, geological evidence shows that oxygen built up to higher concentrations in the atmosphere. This is known as the **Great Oxygenation Event (GOE)** (Figure 7.5.1). Even though levels were rising, oxygen amounts similar to today's only arose within the last 600 Ma just before the beginning of the Cambrian Period.

Recall that the first fossils that we believe to be eukaryotes date to about 2 Ga, so they appeared during the GOE. Also, recall that all extant eukaryotes descended from an ancestor with mitochondria. These organelles were first observed by scientists in the late 1800s, where they were described as somewhat worm-shaped structures that moved around in the cell. Some early observers suggested that they might be bacteria living inside host cells, but these hypotheses remained unknown or rejected in most scientific communities.

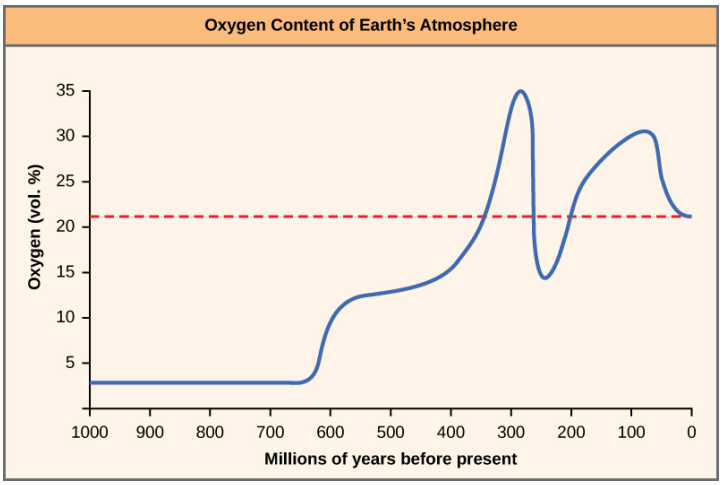


Figure 7.5.1: The oxygen concentration in Earth's atmosphere rose sharply around 300 million years ago. The red dotted line indicates current levels of oxygen in the atmosphere for reference.

Endosymbiotic Theory

As cell biology developed in the twentieth century, it became clear that mitochondria were the organelles responsible for producing ATP using aerobic respiration. In the 1960s, biologist Lynn Margulis proposed the **endosymbiotic theory**, suggesting that eukaryotes were the product of one cell engulfing another. In the proposed model, once engulfed, the two cells continued to live together and evolved co-dependence so that they could no longer live independently of one another. Although Margulis' work initially was met with resistance, this once-revolutionary hypothesis is now widely accepted, with work progressing on uncovering the steps involved in this evolutionary process and the key players involved.

Broadly, it has become clear that many of the nuclear genes and the molecular machinery responsible for replication and the expression of those genes appear closely related to those in Archaea. On the other hand, the metabolic organelles and genes responsible for many energy-harvesting processes had their origins in bacteria.

Much remains to be clarified about how this relationship occurred; this continues to be an exciting field of discovery in biology. For instance, it is not known whether the endosymbiotic event that led to mitochondria occurred before or after the host cell had a nucleus. Such organisms would be among the extinct precursors of the last common ancestor of all eukaryotes.

Video





This 8-minute video provides an overview of the steps in the evolution of eukaryotes from prokaryotes. Question after watching: Which organelle do you think evolved first: chloroplasts that photosynthesize or mitochondria that extract energy from reduced chemicals using oxygen? What is your rationale?

Evidence for Endosymbiosis: Mitochondria

One of the major features distinguishing prokaryotes from eukaryotes is the presence of mitochondria. Eukaryotic cells may contain anywhere from one to several thousand mitochondria, depending on the cell's level of energy consumption. Each mitochondrion measures 1 to 10 or greater micrometers (μm) in length and exists in the cell as an organelle that can be ovoid, worm-shaped, or intricately branched (Figure 7.5.2).

Mitochondria arise from the division of existing mitochondria; they may fuse together; and they may be moved around inside the cell by interactions with the cytoskeleton. However, mitochondria cannot survive outside the cell. As the atmosphere was oxygenated by photosynthesis, and as successful aerobic prokaryotes evolved, evidence suggests that an ancestral cell with some membrane compartmentalization engulfed a free-living aerobic prokaryote, specifically an alpha-proteobacterium, thereby giving the host cell the ability to use oxygen to release energy stored in nutrients.

Alpha-proteobacteria are a large group of bacteria that includes species symbiotic with plants, disease organisms that can infect humans via ticks, and many free-living species that use light for energy. Several lines of evidence support that mitochondria are

derived from this endosymbiotic event. Most mitochondria are shaped like alpha-proteobacteria and are surrounded by two membranes, which would result when one membrane-bound organism was engulfed into a vacuole by another membrane-bound organism. The mitochondrial inner membrane is extensive and involves substantial infoldings called cristae that resemble the textured, outer surface of alpha-proteobacteria. The matrix and inner membrane are rich with the enzymes necessary for aerobic respiration.

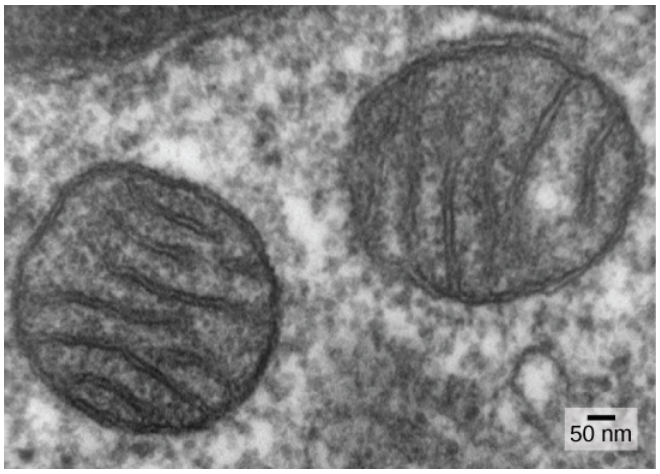


Figure 7.5.2: In this transmission electron micrograph of mitochondria in a mammalian lung cell, the cristae, infoldings of the mitochondrial inner membrane, can be seen in cross-section. (credit: Louise Howard)

Mitochondria divide independently by a process that resembles binary fission in prokaryotes. Specifically, mitochondria are not formed from scratch (de novo) by the eukaryotic cell; they reproduce within it and are distributed with the cytoplasm when a cell divides or two cells fuse. Therefore, although these organelles are highly integrated into the eukaryotic cell, they still reproduce as if they are independent organisms within the cell. However, their reproduction is synchronized with the activity and division of the cell. Mitochondria have their own (usually) circular DNA chromosome that is stabilized by attachments to the inner membrane and carries genes like genes expressed by alpha-proteobacteria. Mitochondria also have special ribosomes and transfer RNAs that resemble these components in prokaryotes. These features all support that mitochondria were once free-living prokaryotes.

Mitochondria that carry out aerobic respiration have their own genomes, with genes similar to those in alpha-proteobacteria. However, many of the genes for respiratory proteins are located in the nucleus. When these genes are compared to those of other organisms, they appear to be of alpha-proteobacterial origin. Additionally, in some eukaryotic groups, such genes are found in the mitochondria, whereas in other groups, they are found in the nucleus. This has been interpreted as evidence that genes have been transferred from the endosymbiont chromosome to the host genome. This loss of genes by the endosymbiont is probably one explanation why mitochondria cannot live without a host.

Some living eukaryotes are anaerobic and cannot survive in the presence of oxygen. Some appear to lack organelles that could be recognized as mitochondria. In the 1970s to the early 1990s, many biologists suggested that some of these eukaryotes were descended from ancestors whose lineages had diverged from the lineage of mitochondrion-containing eukaryotes before endosymbiosis occurred. However, later findings suggest that reduced organelles are found in most, if not all, anaerobic eukaryotes, and that all eukaryotes appear to carry some genes in their nuclei that are of mitochondrial origin. In addition to the aerobic generation of ATP, mitochondria have several other metabolic functions. One of these functions is to generate clusters of iron and sulfur that are important cofactors of many enzymes. Such functions are often associated with the reduced mitochondrion-derived organelles of anaerobic eukaryotes. Therefore, most biologists now accept that the last common ancestor of eukaryotes had mitochondria.

Evidence of Endosymbiosis: Plastids

Some groups of eukaryotes are photosynthetic. Their cells contain, in addition to the standard eukaryotic organelles, another kind of organelle called a plastid. When such cells are carrying out photosynthesis, their plastids are rich in the pigment chlorophyll *a* and a range of other pigments, called **accessory pigments**, which are involved in harvesting energy from light. Photosynthetic plastids are called **chloroplasts** (Figure 7.5.3).

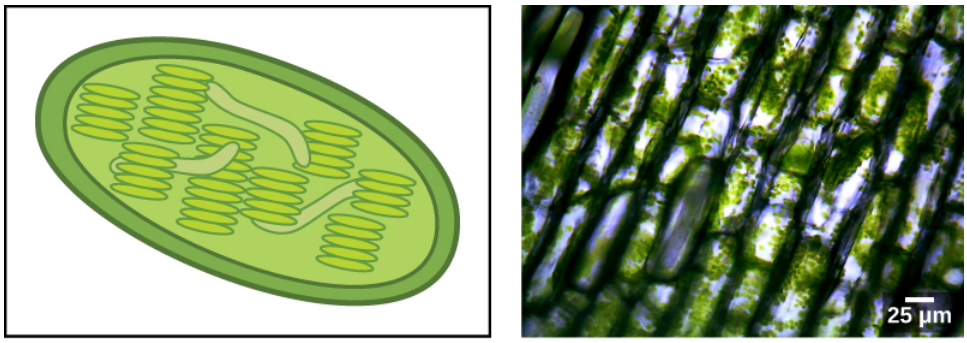


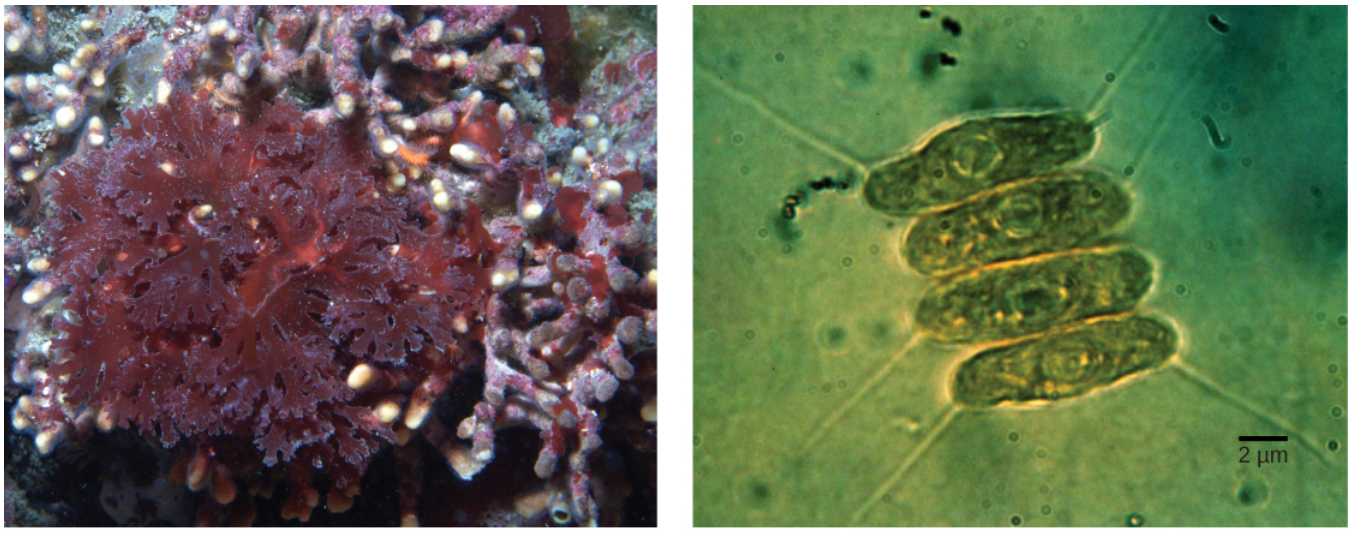
Figure 7.5.3: (a) This chloroplast cross-section illustrates its elaborate inner membrane organization. Stacks of thylakoid membranes compartmentalize photosynthetic enzymes and provide scaffolding for chloroplast DNA. (b) In this micrograph of *Elodea* sp., the chloroplasts can be seen as small green spheres. (credit b: modification of work by Brandon Zierer; scale-bar data from Matt Russell)

Like mitochondria, plastids appear to have an endosymbiotic origin. This hypothesis was also championed by Lynn Margulis. Plastids are derived from cyanobacteria that lived inside the cells of an ancestral, aerobic, heterotrophic eukaryote. This is called primary endosymbiosis, and plastids of primary origin are surrounded by two membranes. This likely happened twice in the history of eukaryotes.

Cyanobacteria are a group of Gram-negative bacteria with all the conventional structures of the group. However, unlike most prokaryotes, they have extensive, internal membrane-bound sacs called thylakoids. Chlorophyll is a component of these membranes, as are many of the proteins of the light reactions of photosynthesis (Figure 7.5.4). Cyanobacteria also have the peptidoglycan wall and lipopolysaccharide layer associated with Gram-negative bacteria.

Chloroplasts of primary origin have thylakoids, a circular DNA chromosome, and ribosomes like those of cyanobacteria. Each chloroplast is surrounded by two membranes. The outer membrane surrounding the plastid is thought to be derived from the vacuole in the host, and the inner membrane is thought to be derived from the plasma membrane of the symbiont.

There is also, as with the case of mitochondria, strong evidence that many of the genes of the endosymbiont were transferred to the nucleus. Plastids, like mitochondria, cannot live independently outside the host. In addition, like mitochondria, plastids are derived from the division of other plastids and never built from scratch. Researchers have suggested that the endosymbiotic event that led to the engulfing of the chloroplast ancestor occurred 1 to 1.5 billion years ago, at least 500 million years after the fossil record suggests that eukaryotes were present.



(a) (b)

Figure 7.5.4: (a) Red algae and (b) green algae (visualized by light microscopy) share similar DNA sequences with photosynthetic cyanobacteria. Scientists speculate that, in a process called endosymbiosis, an ancestral prokaryote engulfed a photosynthetic cyanobacterium that evolved into modern-day chloroplasts. (credit a: modification of work by Ed Bierman; credit b: modification of work by G. Fahnenstiel, NOAA; scale-bar data from Matt Russell)

Optional Activity

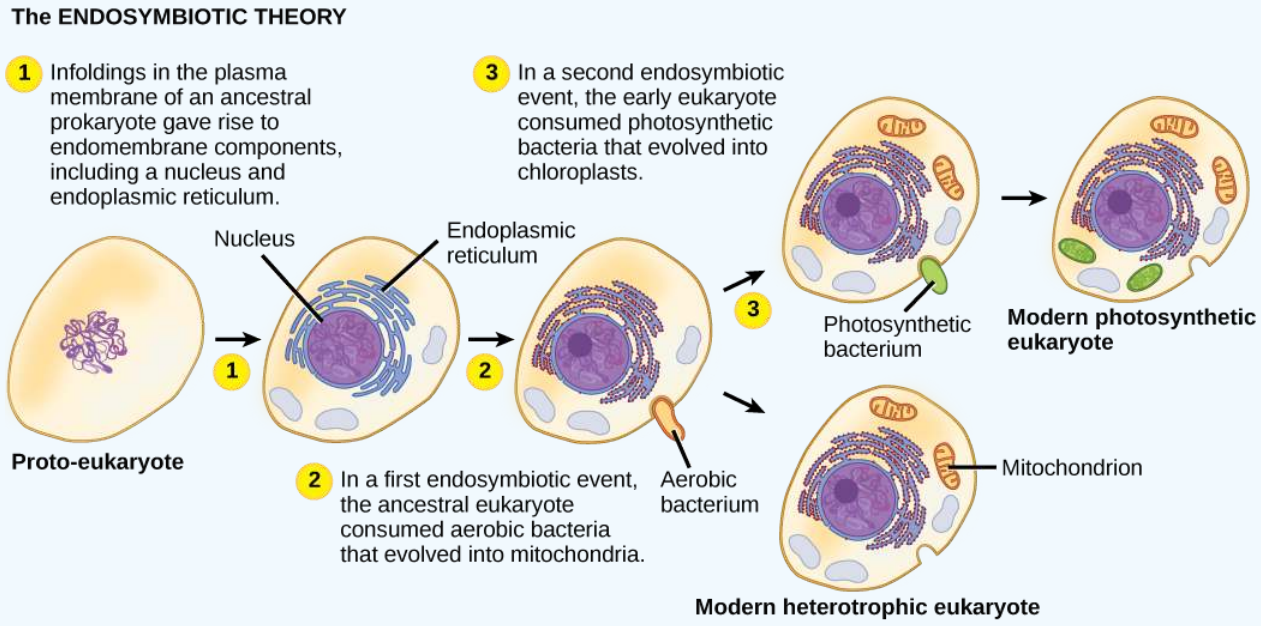


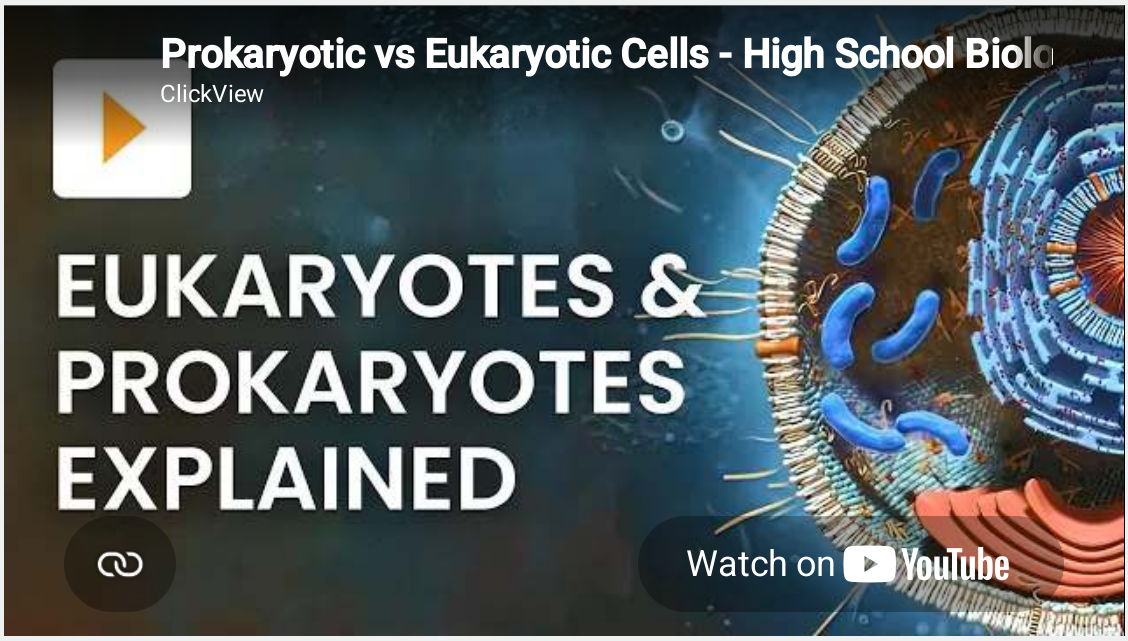
Figure 7.5.5: The first eukaryote may have originated from an ancestral prokaryote that had undergone membrane proliferation, compartmentalization of cellular function (into a nucleus, lysosomes, and an endoplasmic reticulum), and the establishment of endosymbiotic relationships with an aerobic prokaryote, and, in some cases, a photosynthetic prokaryote, to form mitochondria and chloroplasts, respectively.

What evidence is there that mitochondria were incorporated into the ancestral eukaryotic cell before chloroplasts?

Answer

All eukaryotic cells have mitochondria, but not all eukaryotic cells have chloroplasts.

Video





This 4.5-minute video provides a quick overview of the differences between prokaryotes and eukaryotes. Question after watching: What do the characteristics contained in both prokaryotes and eukaryotes tell you about the evolution of life on earth?

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7.6: Systematics and Classification

Systematics and Classification

- Please read and watch the following Mandatory Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 45 minutes.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- State the theoretical basis for modern classification systems
- Recognize and write scientific names using the binomial classification system

The Levels of Classification

Taxonomy (which means “arrangement law” in Latin) is the science of classifying organisms to construct internationally-shared classification systems with each organism placed into increasingly more inclusive groupings. Taxonomic classification divides species into a hierarchical system beginning with a **domain** (Bacteria, Archaea, and Eukarya) and ending with a single species. Within each domain is a second level called a **kingdom** (Archaea, Bacteria, Protista, Fungi, Plantae, and Animalia). Each domain contains several kingdoms. Within kingdoms, the subsequent categories of increasing specificity are phylum, class, order, family, genus, and species.

Think about how a grocery store is organized. One large space is divided into departments, such as produce, dairy, and meats. Then each department is further divided into aisles, then each aisle into categories and brands, and then, finally, a single product. This organization from larger to smaller, more-specific categories is called a hierarchical system.

As an example, the classification levels for the domestic dog are shown in Figure 7.6.1. The group at each level is called a taxon (plural: taxa). In other words, for the dog, Carnivora is the taxon at the order level, Canidae is the taxon at the family level, and so forth. Organisms also have a common name that people typically use, such as domestic dog, or wolf.

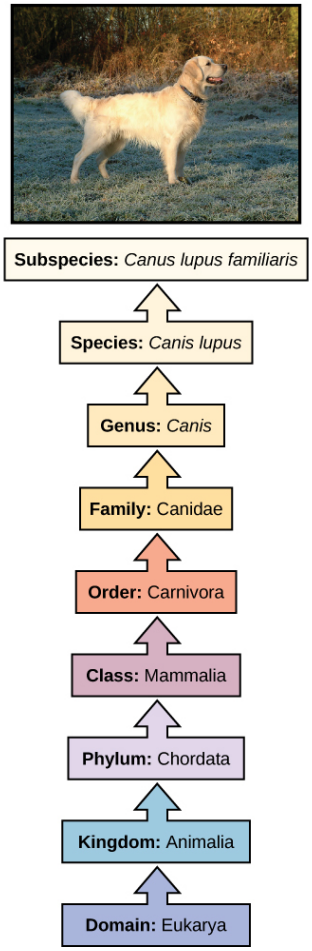


Figure 7.6.1: The taxonomic classification system uses a hierarchical model to organize living organisms into increasingly specific categories. The common dog, *Canis lupus familiaris*, is a subspecies of *Canis lupus*, which also includes the wolf and dingo.

Scientists refer to an organism by its genus and species names together, commonly called a scientific name, or Latin name. This two-name system is called binomial nomenclature. The scientific name of the wolf is therefore *Canis lupus*. A recent study of the DNA of domestic dogs and wolves suggests that the domestic dog is a subspecies of the wolf, not its own species, thus it is given an extra name to indicate its subspecies status, *Canis lupus familiaris*. Subspecies are members of the same species that are capable of mating and producing viable offspring, but they are considered separate subspecies due to geographic isolation, behavioral isolation, or other factors.

The full name of an organism technically has eight terms. Dogs, for example, are technically: Eukarya, Animalia, Chordata, Mammalia, Carnivora, Canidae, *Canis*, and *lupus*. Notice that each name is capitalized except for species and that genus and species names are italicized. Scientists generally refer to an organism only by its genus and species, which is its two-word scientific name, in what is called **binomial nomenclature**. Therefore, the scientific name of the dog is *Canis lupus*. Dogs share a domain (Eukarya) with the widest diversity of organisms, including plants and butterflies.

Video



This 7-minute video explores how life is organized using binomial nomenclature and some examples. Question after watching: Can you come up with a mnemonic device to remember the categories of classification?

Figure 7.6.2 also shows how taxonomic levels move toward specificity. Notice how within the domain we find the dog grouped with the widest diversity of organisms. These include plants and other organisms not pictured, such as fungi and protists. The organisms become more similar at each sublevel because they are more closely related. Before Darwin's theory of evolution was developed, naturalists sometimes classified organisms using arbitrary similarities, but since the theory of evolution was proposed in the 19th-century, biologists work to make the classification system reflect evolutionary relationships. This means all members of a taxon should have a common ancestor and be more closely related to each other than to members of other taxa. Historically, scientists classified organisms using physical characteristics, but as DNA technology developed, more precise relationships have been determined.

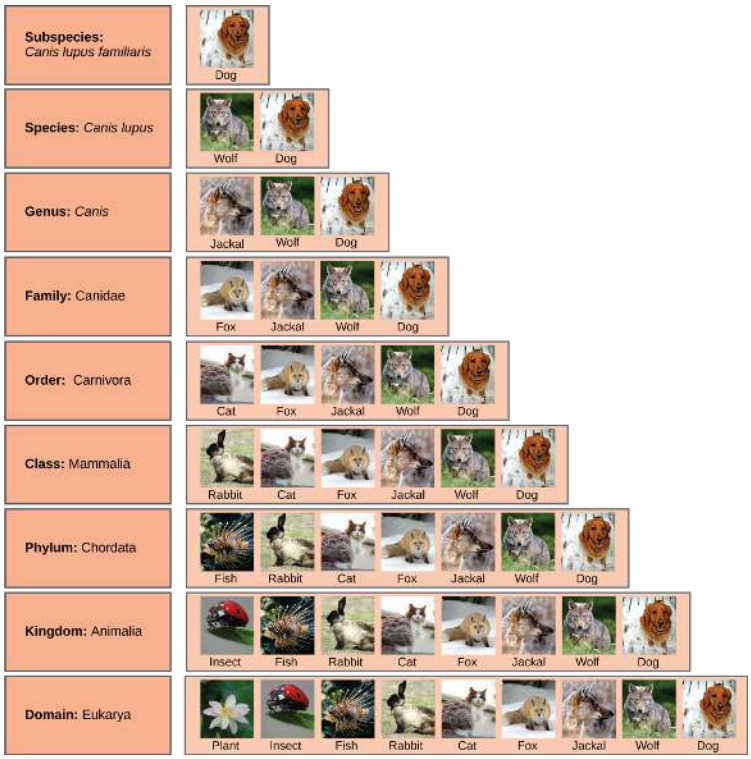


Figure 7.6.2: At each sublevel in the taxonomic classification system, organisms become more similar. Dogs and wolves are the same species because they can breed and produce viable offspring, but they are different enough to be classified as different subspecies. (credit “plant”: modification of work by "berduchwal"/Flickr; credit “insect”: modification of work by Jon Sullivan; credit “fish”: modification of work by Christian Mehlführer; credit “rabbit”: modification of work by Aidan Wojtas; credit “cat”: modification of work by Jonathan Lidbeck; credit “fox”: modification of work by Kevin Bacher, NPS; credit “jackal”: modification of work by Thomas A. Hermann, NBII, USGS; credit “wolf” modification of work by Robert Dewar; credit “dog”: modification of work by "digital_image_fan"/Flickr)

? Optional Activity

Question: Refer to Figure 7.6.2. At what levels are cats and dogs considered to be part of the same group?

Answer

Cats and dogs are part of the same group at five levels: both are in the domain Eukarya, the kingdom Animalia, the phylum Chordata, the class Mammalia, and the order Carnivora.

Video





In this 12-minute video, the science of taxonomy is explained, including an overview of the major kingdoms of life. Question after watching: Using your favorite organism, find its scientific name and try placing it into its appropriate classifications.

Optional Activity

List the different levels of the taxonomic classification system.

Answer

From most inclusive to least inclusive: domain, kingdom, phylum, class, order, family, genus, species.

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7.7: Phylogeny and Cladistics

Phylogeny and Cladistics

- Please read and watch the following Mandatory Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 3 hours.
- Bolded terms are located at the end of the unit in the Glossary. There is also a Unit Summary at the end of the Unit.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Explain the purpose of cladistics
- Design a cladogram
- Recognize and interpret a phylogenetic tree
- Explain a phylogenetic tree's components and purpose

Introduction to Phylogeny

All life on Earth evolved from a common ancestor. Biologists map how organisms are related by constructing **phylogenetic trees**. Phylogenetic trees are diagrams used to reflect evolutionary relationships among organisms or groups of organisms. In other words, a "tree of life" can be constructed to illustrate when different organisms evolved and to show the relationships among different organisms, as shown in Figure 7.7.1. Notice that from a single point, the three domains of Archaea, Bacteria, and Eukarya diverge and then branch repeatedly. The small branch that plants and animals (including humans) occupy in this diagram shows how recently these groups had their origin compared with other groups. A **phylogeny** is the evolutionary history and the relationships among a species or group of species. The study of organisms with the purpose of deriving their relationships is called **systematics**.

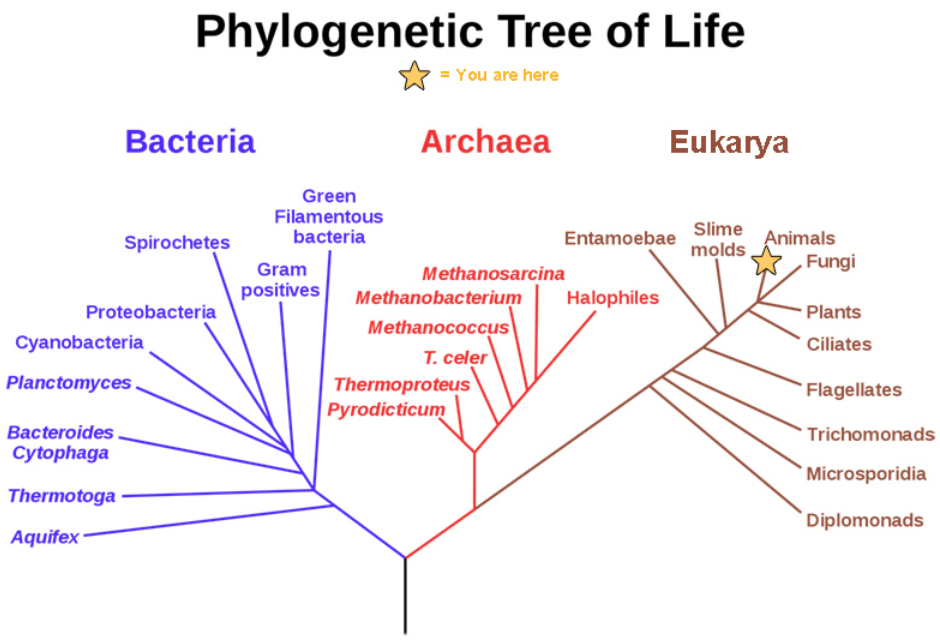


Figure 7.7.1: In the evolution of life on Earth, the three domains of life—Archaea, Bacteria, and Eukarya—branch from a single point. (credit: modification of work by Eric Gaba)

Understanding Phylogeny

Two Measures of Similarity

Organisms that share similar physical features *and* genetic sequences tend to be more closely related than those that do not. Features that overlap both morphologically and genetically are referred to as homologous structures; the similarities stem from common evolutionary paths. For example, as shown in Figure 7.7.2, the bones in the wings of bats and birds, the arms of humans, and the foreleg of a horse are homologous structures. Notice the structure is not simply a single bone, but rather a grouping of several bones arranged in a similar way in each organism even though the elements of the structure may have changed shape and size.

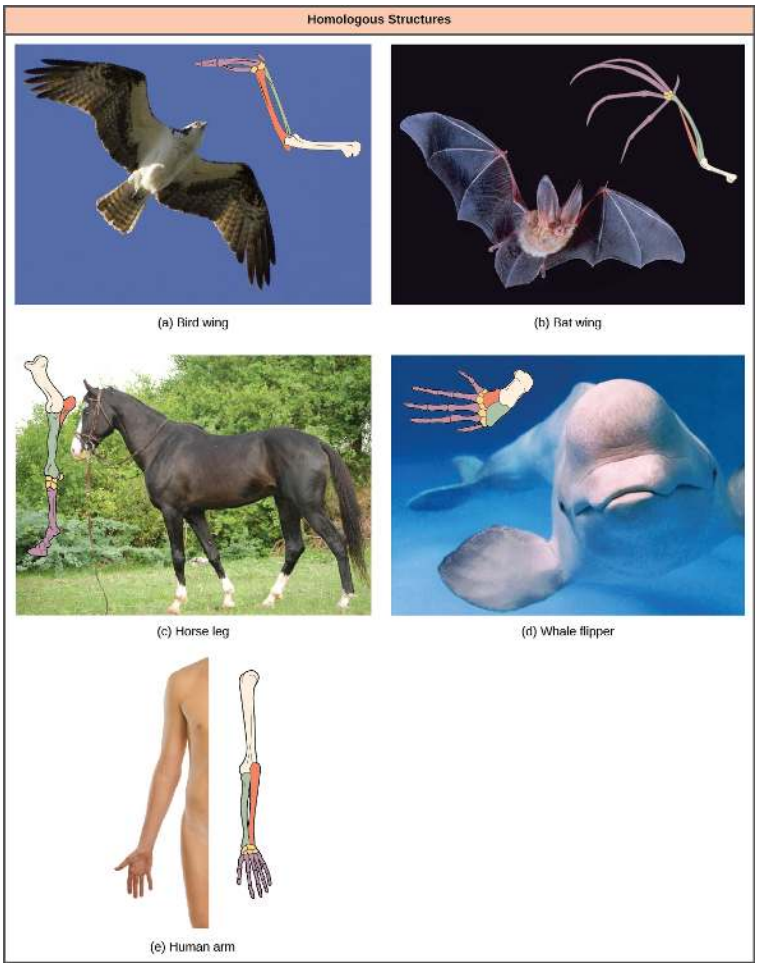


Figure 7.7.2: Bat and bird wings, the foreleg of a horse, the flipper of a whale, and the arm of a human are homologous structures, with similar bones indicated by the same color. This indicates that bats, birds, horses, whales, and humans share a common evolutionary past. (credit a photo: modification of work by Steve Hillebrand, USFWS; credit b photo: modification of work by U.S. BLM; credit c photo: modification of work by Virendra Kankariya; credit d photo: modification of work by Russian Gov./Wikimedia Commons)

Misleading Appearances

Some organisms may be very closely related, even though a minor genetic change caused a major morphological difference to make them look quite different. For example, chimpanzees and humans, the skulls of which are shown in Figure 7.7.3 are very similar genetically, sharing 99 percent[1] of their genes. However, chimpanzees and humans show considerable anatomical differences, including the degree to which the jaw protrudes in the adult and the relative lengths of our arms and legs.



Figure 7.7.3: (a) The chimpanzee jaw protrudes to a much greater degree than (b) the human jaw. (credit a: modification of work by "Pastorius"/Wikimedia Commons)

However, unrelated organisms may be distantly related yet appear very much alike, usually because common adaptations to similar environmental conditions evolved in both independently. An example is the streamlined body shapes, the shapes of fins and appendages, and the shape of the tails in fishes (which are from the fish taxon) and whales (which are from the mammal taxon). These structures bear superficial similarity because they are adaptations to moving and maneuvering in the same environment—water. When a characteristic that is similar occurs by adaptive convergence (convergent evolution), and not because of a close evolutionary relationship, it is called an analogous structure.

In another example, insects use wings to fly like bats and birds. We call them all wings because they perform the same function and have a superficially similar form, but the embryonic origin of the three wings is different. The difference in the development, or embryogenesis, of the wings in each case is a signal that insects versus bats or birds do not share a common ancestor that had a wing. The wing structures, shown in Figure 7.7.4 evolved independently in the two lineages (insects versus vertebrates).

Similar traits can be either homologous or analogous. Homologous traits share an evolutionary path that led to the development of that trait. Analogous traits may look similar but they do not share a common evolutionary origin. Scientists must determine which type of similarity a feature exhibits to decipher the phylogeny of the organisms being studied.

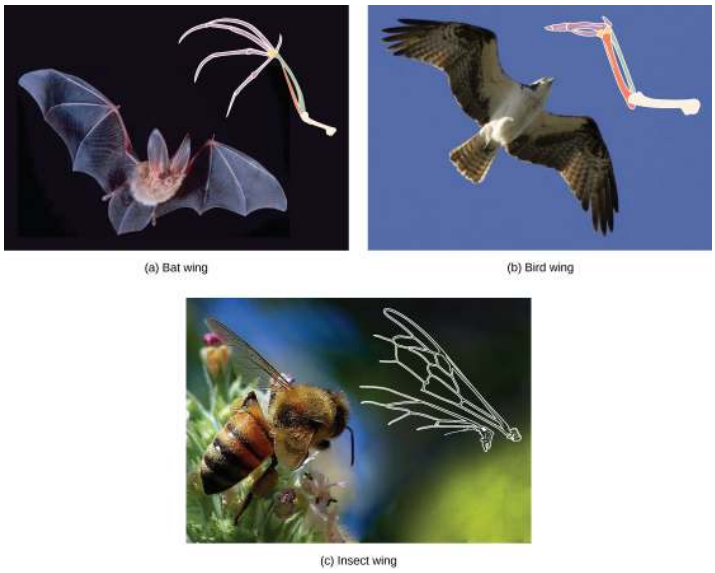


Figure 7.7.4: The wing of a honeybee is similar in shape to a bird wing and a bat wing and it serves the same function (flight). The bird and bat wings are homologous structures. However, the honeybee wing has a different structure (it is made of a chitinous exoskeleton, not a boney endoskeleton) and embryonic origin. The bee versus bird or bat wing types illustrate an analogy—similar structures that do not share an evolutionary history. (credit a photo: modification of work by U.S. BLM; credit b: modification of work by Steve Hillebrand, USFWS; credit c: modification of work by Jon Sullivan)

Optional Activity

Which statement about analogies is correct?

a. They occur only as errors.
b. They are synonymous with homologous traits.
c. They are derived due to similar environmental constraints.
d. They are a form of mutation.

Answer

c. They are derived due to similar environmental constraints.

Molecular Comparisons

With the advancement of DNA technology, the area of **molecular systematics**, which describes the use of information on the molecular level including DNA sequencing, has blossomed. New analysis of molecular characters not only confirms many earlier classifications, but also uncovers previously made errors based on morphology alone. **Molecular characters** can include differences in the amino-acid sequence of a protein, shapes of a protein, RNA, location of a gene, differences in the individual nucleotide sequence of a gene, or differences in the arrangements of genes. Phylogenies based on molecular characters assume that the more similar the sequences are in two organisms, the more closely related they are. Different genes change evolutionarily at different rates and this affects the level at which they are useful at identifying relationships. Rapidly evolving sequences are useful for determining the relationships among closely related species. More slowly evolving sequences are useful for determining the relationships between distantly related species. To determine the relationships between very different species such as Eukarya and Archaea, the genes used must be very ancient, slowly evolving genes that are present in both groups, such as the genes for ribosomal RNA. Comparing phylogenetic trees using different sequences and finding them similar helps to build confidence in the inferred relationships.

Sometimes two segments of DNA in distantly related organisms randomly share a high percentage of bases in the same locations, causing these organisms to appear closely related when they are not. For example, the fruit fly shares 60 percent of its DNA with humans.[2] These similar sections are those that make fruit flies and humans both eukaryotes and animals. This 60 percent is important but does not tell us as much about why we are different. In this situation, computer-based statistical algorithms have been developed to help identify how far back our common ancestor was, which is difficult, if not impossible with morphology alone. Ultimately, the coupled use of both morphologic and molecular information is most effective in determining phylogeny.

Optional Resource

This Click and Learn describes the process of aligning DNA sequences from different organisms so that they can be compared to one another: https://media.hhmi.org/biointeractive/click/Phylogenetic_Trees/01.html

To navigate this resource, use the forward and back arrows at the top right of the webpage. There will be short videos on most pages. Click on the Play symbol (arrow in a rectangle) to play the video.

Video





This 12.5-minute video discusses some interesting phylogenetic mysteries.
Question after watching: Of the three cases featured, which one helped you understand phylogeny better?

Classification and Phylogeny

Scientists use phylogenetic trees to show the evolutionary pathways and relationships between organisms. The hierarchical classification of groups nested within more inclusive groups is reflected in diagrams. Scientists consider phylogenetic trees to be a hypothesis of the evolutionary past because one cannot go back through time to confirm the proposed relationships. Unlike taxonomy, a phylogenetic tree can be read like a map of evolutionary history.

Scientists apply the concept of **maximum parsimony**, which states that the likeliest order of events is the simplest shortest path. For evolutionary events, this would be the path with the least number of major divergences that correlate with the evidence.

Recent genetic analysis and other advancements have found that some earlier taxonomic classifications do not reflect actual evolutionary relationships, and therefore, changes and updates must be made as new discoveries take place. Recall that phylogenetic trees are hypotheses and are modified as data becomes available. In addition, classification historically has focused on grouping organisms mainly by shared characteristics and does not necessarily illustrate how the various groups relate to each other from an evolutionary perspective. For example, despite the fact that a hippopotamus resembles a pig more than a whale, the hippopotamus may be the closest living relative to the whale. One dramatic and recent example was the breaking apart of

prokaryotic species which, until the 1970s, were all classified as 'bacteria'. Their division into Archaea and Bacteria came about after the recognition that their large genetic differences warranted their separation into two of three fundamental Domains of life.

Phylogenetic Trees

The phylogenetic tree in Figure 7.7.1 illustrates the pathway of evolutionary history. The pathway can be traced from the origin of life to any individual species by navigating through the evolutionary branches between the two points. Also, by starting with a single species and tracing backward to any branch point, the organisms related to it by various degrees of relatedness can be identified.

Many phylogenetic trees have a single branch point at the base representing a **common ancestor** of all the branches in the tree. This is known as a **rooted tree.** The branching from that root indicates evolutionary relationships as in Figure 7.7.6. The point where a split occurs, called a branch point or "**node**", represents where a single lineage evolved into distinct new ones.

A lineage that evolved early from the root and remains unbranched is called **basal taxon**. When two lineages stem from the same node, they are called **sister taxa**. A node with more than two lineages is called a **polytomy** and serves to illustrate where scientists have not definitively determined all relationships. It is important to note that while sister taxa or polytomy share an ancestor, this does not mean that one taxon evolved from the other. The branch point, or split, represents a common ancestor that existed in the past, but that no longer exists. Organisms in two taxa may have split apart at a specific node, but neither taxon gave rise to the other.

Rooted phylogenetic trees can serve as a pathway to understanding evolutionary history. The pathway can be traced from the origin of life to any individual species by navigating through the evolutionary branches between the two points. Also, by starting with a single species and tracing back towards the “trunk” of the tree, one can discover that species’ ancestors, as well as where lineages share a common ancestry. In addition, the tree can be used to study entire groups of organisms.

Another point to mention on phylogenetic tree structure is that *rotation at nodes does not change the information* Figure \(\PageIndex{7}\). For example, if a node was rotated and the taxon order changed, this would not alter the information because the evolution of each taxon from the node was independent of the other.

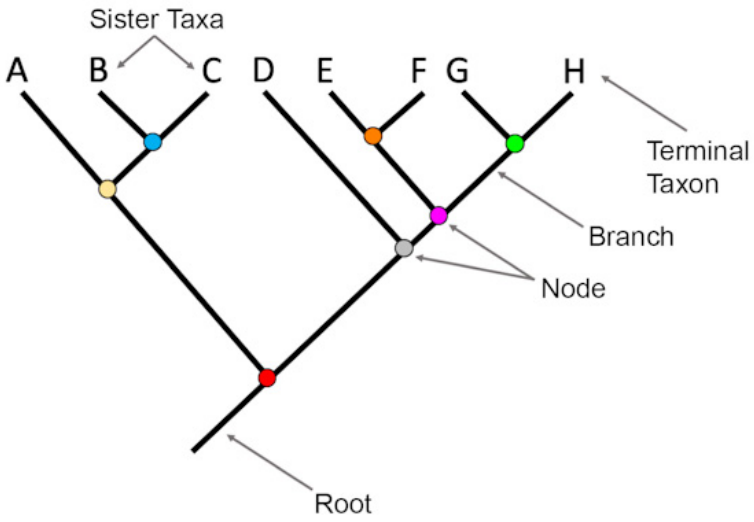


Figure 7.7.6: Parts of a phylogenetic tree, including terminal taxa, sister taxa, root, branch, and node. Image by Jonathan R. Hendricks (CC-BY-SA 4.0).

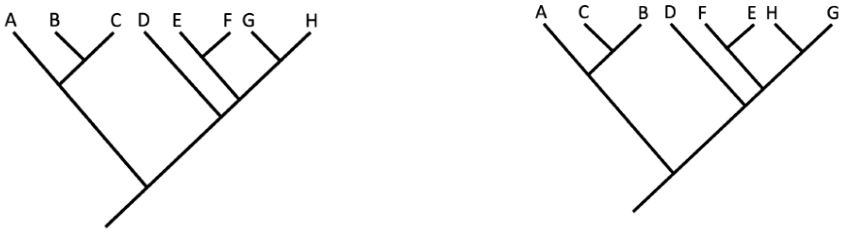
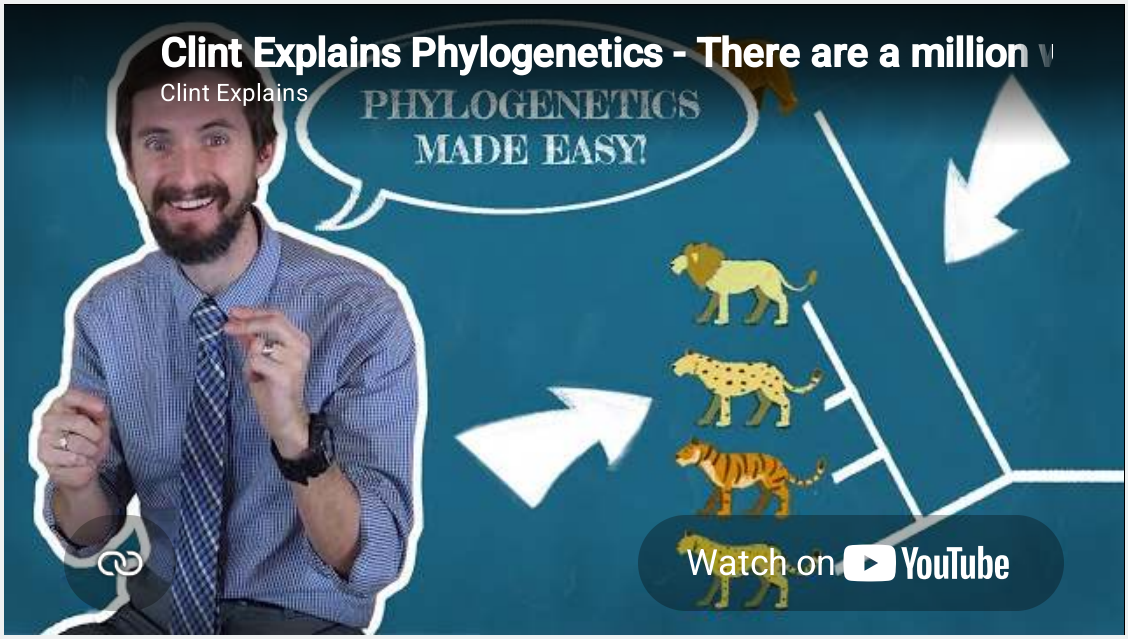
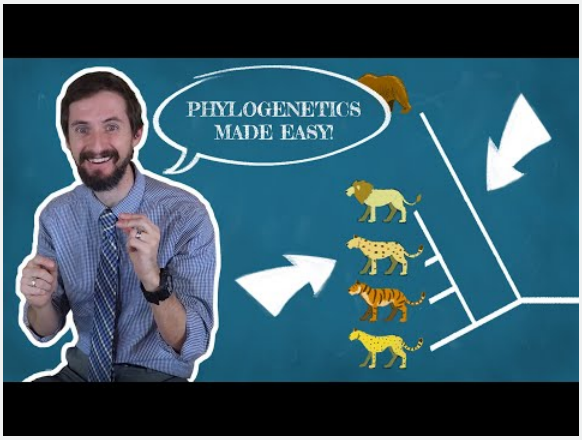


Figure \(\PageIndex{7}\):
Branches may be rotated about nodes without any change in the hypothesized relationships depicted on a tree diagram. There is no difference in the evolutionary relationships being depicted between these two trees. Images by Jonathan R. Hendricks (CC-BY-SA 4.0).

Video





This 8-minute video explains phylogenetics.
Question after watching:
Which big cat is most closely related to the cheetah?

Figure 7.7.8 is a rooted tree for the modern great apes. The two species of orangutans are sister taxa. The three branches leading to the gorilla subspecies are a polytomy. The names of the species that are at the tip of the branches are co-existing species in the current time. The common ancestor that gave rise to two currently existing species was neither of these current species, but rather an ancestral species to both that no longer exists. For example, humans did not evolve from bonobos or chimpanzees (nor did chimpanzees evolve from humans) although they are our closest living relatives. Humans, bonobos, and chimpanzees all evolved from a common ancestor that lived, scientists believe, six million years ago and looked different from modern chimpanzees, bonobos, AND humans.

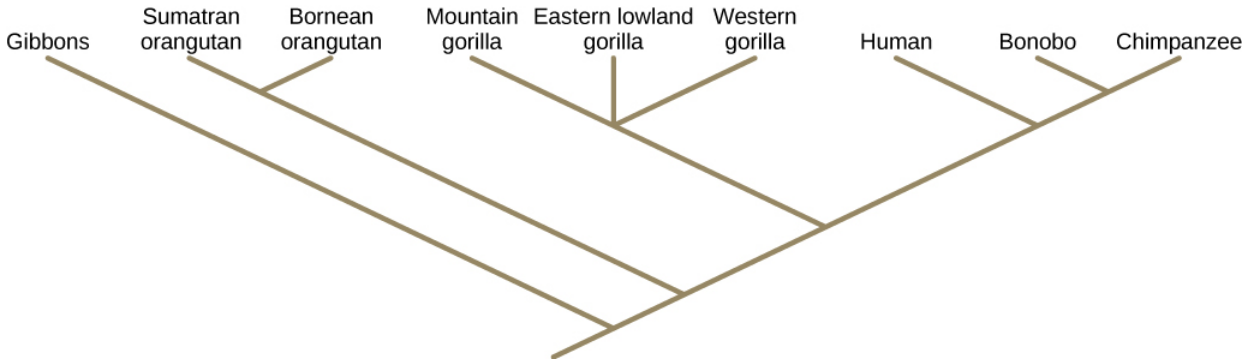


Figure 7.7.8: This phylogenetic tree is rooted and shows how different organisms, in this case the species and subspecies of living apes, evolved from a common ancestor.

The nodes and the branches in phylogenetic tree structure imply evolutionary change. Sometimes the significant adaptive changes are identified on a branch or node. For example, in Figure 7.7.9, the node that gives rise to the mammal and reptile lineage from the frog lineage shows the origin of the amniotic egg character. Also, the node that gives rise to organisms with legs is indicated at the common ancestor of mammals, reptiles, amphibians, and jawed fishes.

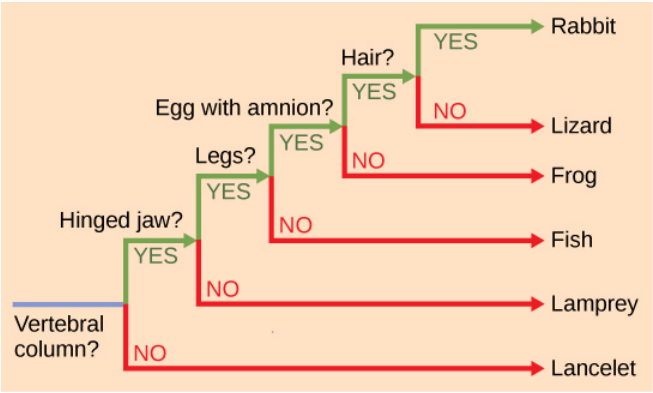


Figure 7.7.9: This phylogenetic tree is rooted by an organism that lacked a vertebral column. At each branch point, organisms with different characters are placed in different groups.

Understanding Phylogenetic Trees

One of the most common forms of a phylogenetic tree is a **cladogram**, seen in Figures 7.7.10 and 7.7.11. To begin this diagram, scientists often organize the homologous and analogous traits of various organisms using a system called **cladistics**. This system sorts organisms into **clades**: groups of organisms that descended from a single ancestor. For example, all organisms in the orange region in Figure 7.7.10 evolved from a single ancestor that had amniotic eggs. Consequently, all these organisms also have amniotic eggs and make a single clade, also called a **monophyletic group**. Clades must include all descendants from a branch point.

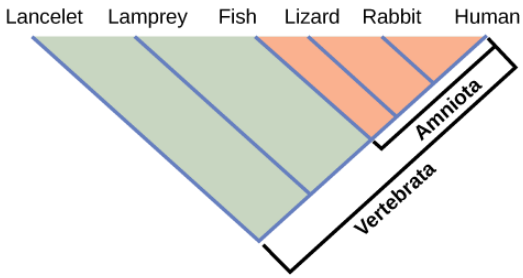


Figure 7.7.10: Lizards, rabbits, and humans all descend from a common ancestor that had an amniotic egg. Thus, lizards, rabbits, and humans all belong to the clade Amniota. Vertebrata is a larger clade that also includes fish and lamprey.

Clades can vary in size depending on which branch point is being referenced. The important factor is that all organisms in the clade or monophyletic group stem from a single point on the tree. This can be remembered because monophyletic breaks down into "mono," meaning one, and "phyletic," meaning evolutionary relationship. Notice in the examples of clades how each clade comes from a single point, whereas the non-clade groups show branches that do not share a single point.

? Optional Activity

On a phylogenetic tree, which term refers to lineages that diverged from the same place?

a. sister taxa
b. basal taxa
c. rooted taxa
d. dichotomous taxa

Ans wer

a. sister taxa

? Optional Activity

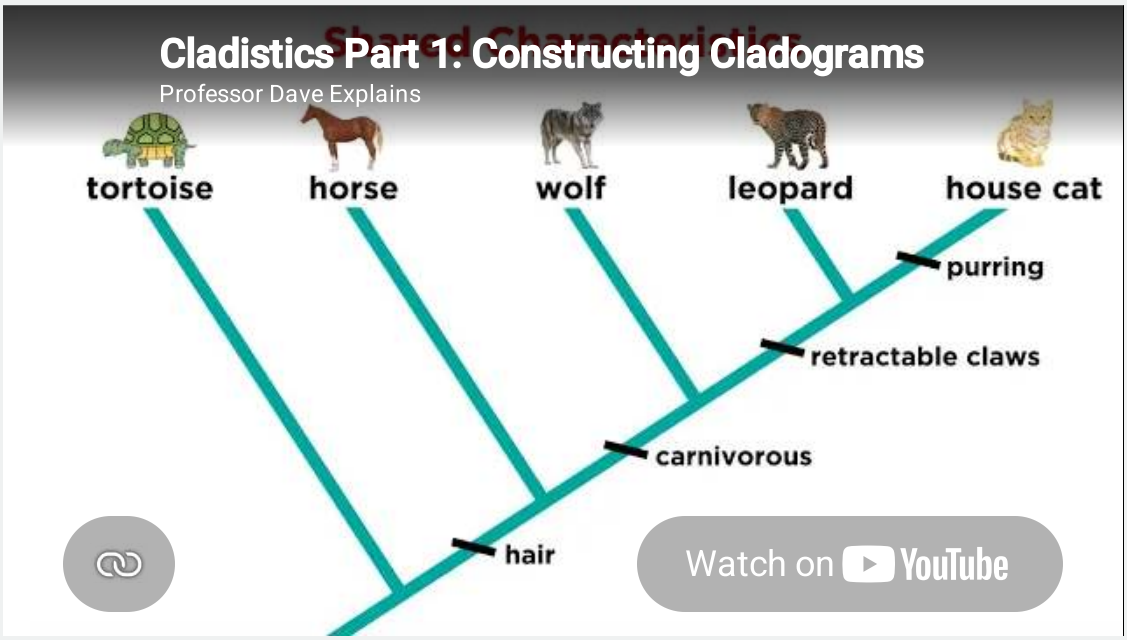
Which animals in the phylogenetic tree in Figure 7.7.10 belong to a clade that includes animals with hair? Which evolved first: hair or the amniotic egg?

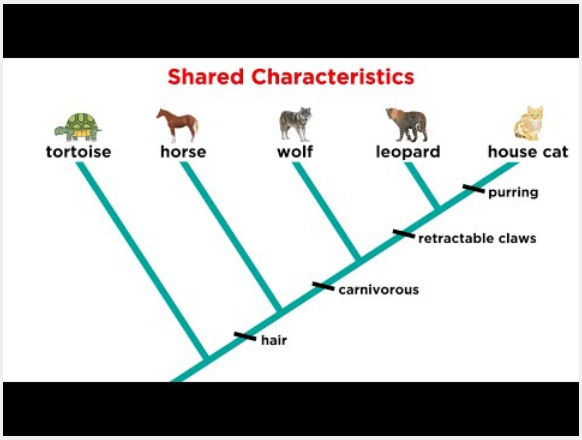
Answer

Rabbits and humans belong in the clade that includes animals with hair. The amniotic egg evolved before hair, because the Amniota clade branches off earlier than the clade that encompasses animals with hair.

https://bio.libretexts.org/@go/page/96549

Video





This 10-minute video is the first part of a sequence that describes how cladograms are created.

Question after watching:

How does science represent the relationships between organisms?

Cladistics and Shared Characteristics

Organisms evolve from common ancestors and then diversify. Scientists use the phrase “descent with modification” because even though related organisms have many of the same characteristics and genetic codes, changes occur.

This pattern repeats as one goes through the phylogenetic tree of life:

1. A change in the genetic makeup of an organism leads to a new trait that becomes prevalent in the group.
2. Many organisms descend from this point and have this trait.
3. New variations continue to arise: some are adaptive and persist, leading to new traits.
4. With new traits, a new branch point is determined (go back to step 1 and repeat).

Cladistics rests on three assumptions.

1. Living things are related by descent from a common ancestor, which is a general assumption of evolution.

2. Speciation occurs by splits of one species into two, never more than two at a time, and at one point in time. This is a simplification but is accepted by most biologists.
3. Traits change enough over time to be considered to be in a different state.

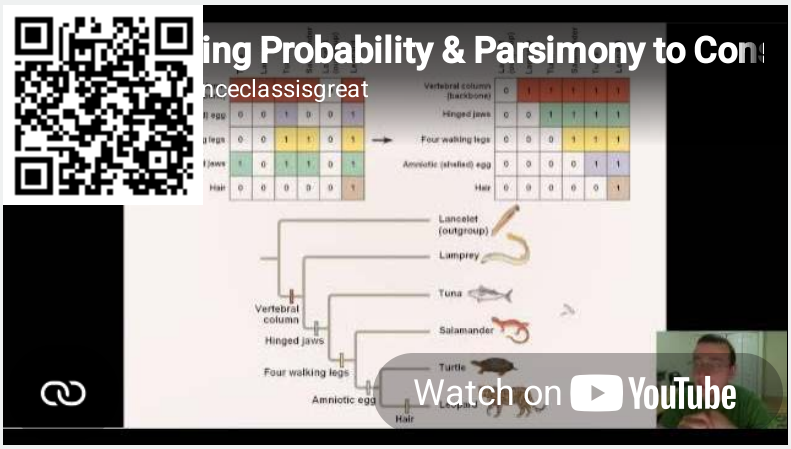
It is also assumed that one can identify the direction of change for an adaptation. In other words, we assume that an amniotic egg is a later character state than non-amniotic eggs. We know this by reference to a group outside the clade: for example, insects have non-amniotic eggs; therefore, this is the older or ancestral character state.

Cladistics compares **ingroups** and **outgroups**. An ingroup (lizard, rabbit and human in our example) is the group of taxa being analyzed in Figure 7.7.10. An outgroup (lancelet, lamprey and fish in our example) is a species or group of species that diverged before the lineage containing the group(s) of interest. By comparing ingroup members to each other and to the outgroup members, we can determine which characteristics are evolutionary adaptations determining the branch points of the ingroup's phylogeny.

If a characteristic is found in all members of a group, it is a **shared ancestral character**: there has been no change in the adaptation during the descent of each member of the clade. Although these traits appear interesting because they unify the clade, in cladistics they are considered not helpful when we are trying to determine the relationships of the members of the clade because every member is the same. In contrast, consider the amniotic egg characteristic of Figure 7.7.10. Only some of the organisms have this trait; to those that do, it is called a **shared-derived character** because this trait derived at some point but does not include all of the ancestors in the tree. This character tells us about the relationships among the members of the clade; it tells us that lizards, rabbits, and humans group more closely together than any of these organisms do with fish, lampreys, and lancelets.

The tricky aspect to shared-ancestral and shared-derived characters is the fact that these terms are relative. The same trait could be either ancestral or derived depending on the diagram being used and the organisms being compared. Scientists find these terms useful when distinguishing between clades during the building of phylogenetic trees, but it is important to remember that their meaning depends on context.

Video



In this 13-minute video, learn how biologists use genetic data to determine relationships among organisms. Question after watching: Are fungi closest to plants or animals, in evolutionary terms? What is the evidence for this?

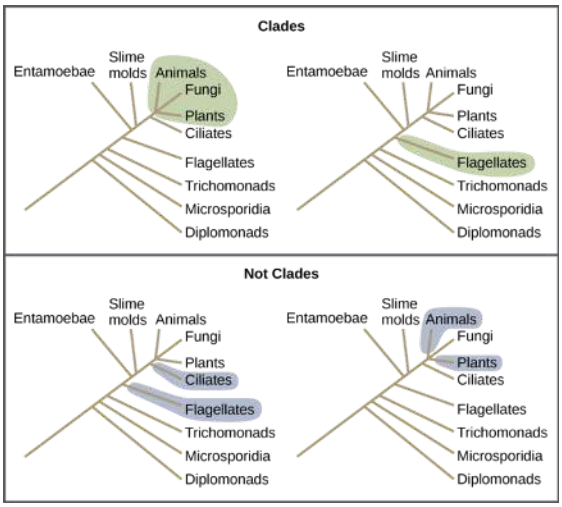


Figure 7.7.11: All the organisms within a clade stem from a single point on the tree. A clade may contain multiple groups, as in the case of animals, fungi, and plants, or a single group, as in the case of flagellates. Groups that diverge at a different branch point, or that do not include all groups in a single branch point, are not considered clades.

? Optional Activity

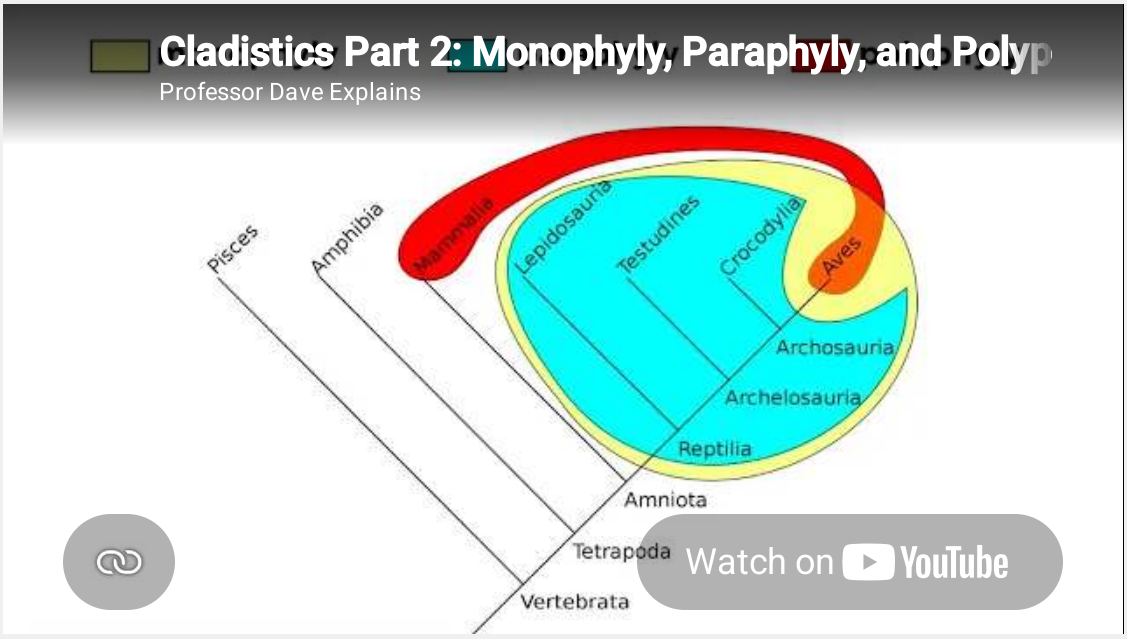
What is true about organisms that are a part of the same clade?

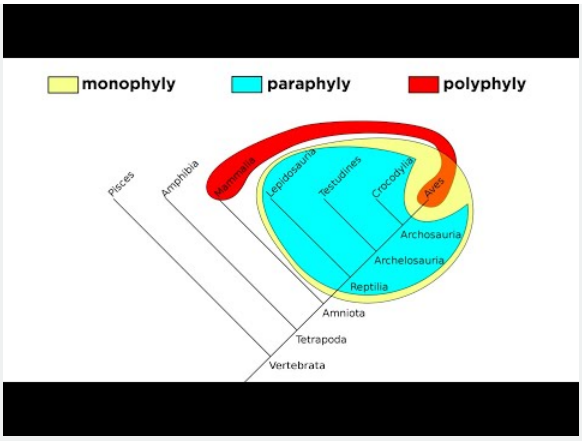
a. They all share the same basic characteristics.
b. They evolved from a shared ancestor.
c. They usually fall into the same classification taxa.
d. They have identical phylogenies.

Answer

b. They evolved from a shared ancestor.

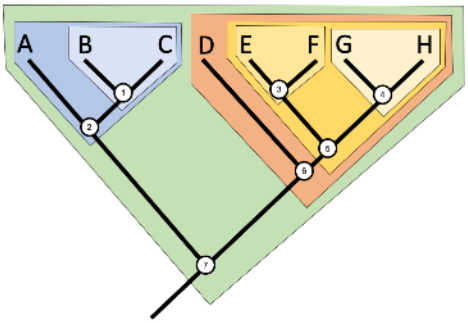
Video





This 6.5-minute video describes clades and their representation on phylogenetic trees.
Question after watching: How can you distinguish between a taxon and a clade?

? Optional Activity



Clades are not mutually exclusive, but rather form nested sets on a tree. Thus, any given taxon can belong to many clades. For example, in the tree above, Taxon B belongs to three clades, a clade defined by Node 1, a more inclusive clade defined by Node 2, and an even more inclusive clade defined by Node 7. Taxon E belongs to four clades defined by Nodes 3, 5, 6, and 7, respectively.

Try to figure out how many clades Taxon A and Taxon H belong to, and determine which nodes define each clade. (Jonathan R. Hendricks; CC-BY-SA 4.0)

Answer

Taxon A belongs to two clades and is defined by Node 2 and, more inclusively, Node 7. Taxon H belongs to four clades and is defined by Nodes (from least to most inclusive) 4, 5, 6, and 7.

Limitations of Phylogenetic Trees

It is easy to assume that more closely related organisms look more alike, and while this is often the case, it is not always true. If two closely related lineages evolved under significantly different surroundings or after the evolution of a major new adaptation, they may look quite different from each other, even more so than other groups that are not as closely related. For example, the phylogenetic tree in Figure 7.7.10 shows that lizards and rabbits both have amniotic eggs, whereas salamanders (within the frog lineage) do not. This means that evolutionarily, lizards and rabbits last shared a common ancestor more recently than lizards and salamanders. Superficially, however, lizards and salamanders appear more similar than lizards and rabbits.

Another aspect of phylogenetic trees is that, unless otherwise indicated, *branches do not show length of time*, they show only the order in time of evolutionary events. In other words, a long branch does not necessarily mean more time passed, nor does a short

branch mean less time passed— unless specified on the diagram. For example, in Figure 7.7.9, the tree does not indicate how much time passed between the evolution of amniotic eggs and hair. What the tree does show is the *order* in which things took place. Again using Figure 7.7.9, the tree shows that the oldest trait is the vertebral column, followed by hinged jaws, and so forth. Remember that any phylogenetic tree is a part of the greater whole, and similar to a real tree, it does not grow in only one direction after a new branch develops. So, for the organisms in Figure 7.7.9, just because a vertebral column evolved does not mean that invertebrate evolution ceased, it only means that a new branch formed. Also, groups that are not closely related, but evolve under similar conditions, may appear more similar to each other than to a close relative.

Why Does Phylogeny Matter?

In addition to enhancing our understanding of the evolutionary history of species, our own included, phylogenetic analysis has numerous practical applications. Two of those applications include understanding the evolution and transmission of disease and making decisions about conservation efforts. A 2010 study[3] of MRSA (methicillin-resistant *Staphylococcus aureus*), an antibiotic-resistant pathogenic bacterium, traced the origin and spread of the strain in the past 40 years. The study uncovered the timing and patterns in which the resistant strain moved from its point of origin in Europe to centers of infection and evolution in South America, Asia, North America, and Australasia. The study suggested that introductions of the bacteria to new populations occurred very few times, perhaps only once, and then spread from that limited number of individuals. This contrasts with the possibility that many individuals had carried the bacteria from one place to another. This result suggests that public health officials should concentrate on quickly identifying the contacts of individuals infected with a new strain of bacteria to control its spread.

A second area of usefulness for phylogenetic analysis is in conservation. Biologists argue that it is important to protect species throughout a phylogenetic tree rather than just those from one branch of the tree. Doing this preserves more of the variation produced by evolution. This is important because genetic variation makes a species more robust to disruption by being more likely to have some individuals with the traits necessary to survive a change in the environment. For example, conservation efforts should focus on a single species without sister species rather than other species that have a cluster of close sister species that recently evolved. If a single evolutionarily distinct species goes extinct, a disproportionate amount of variation from the tree will be lost compared to one species in the cluster of closely related species.

A study published in 2007[4] made recommendations for the conservation of mammal species worldwide based on how evolutionarily distinct and at risk of extinction they are. The study found that their recommendations differed from priorities based on simply the level of extinction threat to the species. The study recommended protecting some threatened and valued large mammals such as the orangutans, the giant and lesser pandas, and the African and Asian elephants. But they also found that some much lesser-known species should be protected based on how evolutionary distinct they are. These include several rodents, bats, shrews, and hedgehogs. In addition, there are some critically endangered species that did not rate as very important in evolutionary distinctiveness including species of deer mice and gerbils. While many criteria affect conservation decisions, preserving phylogenetic diversity provides an objective way to protect the full range of diversity generated by evolution.

Choosing the Right Relationships

Constructing a phylogenetic tree, or cladogram, from the character data is a monumental task that is usually left up to a computer. The computer draws a tree such that all clades share the same list of derived characters. However, there are decisions to be made. For example, what if a species present in a clade is supported by all of the shared derived characters for that clade except one? One conclusion is that the trait evolved in the ancestor, but then changed back in that one species. Also, a character state that appears in two clades must be assumed to have evolved independently in those clades. These inconsistencies are common in trees drawn from character data and complicate the decision-making process about which tree most closely represents the real relationships among the taxa.

To aid in the tremendous task of choosing the best tree, scientists use maximum parsimony, which means they assume that that events occurred in the simplest, most obvious way. This means that the “best” tree is the one with the fewest number of character reversals, the fewest number of independent character changes, and the fewest number of character changes throughout the tree. Computer programs search through all of the possible trees to find the small number of trees with the simplest evolutionary pathways.

? Optional Activity

Why do scientists apply the concept of maximum parsimony?

a. to decipher accurate phylogenies
b. to eliminate analogous traits
c. to identify mutations in DNA codes
d. to locate homoplasies

Answer

a. to decipher accurate phylogenies

Footnotes

1. 1 Gibbons, A. (2012, June 13). *Science Now*. Retrieved from news.sciencemag.org/scienceno...sequenced.html
2. 2 *Background on comparative genomic analysis*. (2002, December). Retrieved from http://www.genome.gov/10005835
3. 3 Harris, S.R. et al. 2010. Evolution of MRSA during hospital transmission and intercontinental spread. *Science* 327:469–474.
4. 4 Isaac NJ, Turvey ST, Collen B, Waterman C, Baillie JE (2007) Mammals on the EDGE: Conservation Priorities Based on Thr eat and Phylogeny. PLoS ONE 2(3): e296. doi:10.1371/journal.pone.0000296

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CHAPTER OVERVIEW

Chapter 8: Life Histories

Learning Objectives

- Describe life history theory, the traits typically associated with the study of life histories.
- Explain the role of trade-offs and the principle of allocation in shaping life history traits.
- Explain correlated life history patterns we often observe across species (e.g., the concepts of **r**- versus **K**-selection), and conditions that could favor different life history strategies.
- Describe why organisms experience senescence, and compare and contrast hypotheses of aging.

1: What is life history?

1.1: Scientist Spotlight - Erin Satterthwaite

2: Life History Evolution

3: The Evolution of Aging

4: Semelparity versus Iteroparity

Summary

A species' life history describes the series of events over its lifetime, such as how resources are allocated for growth, maintenance, and reproduction. Life history traits affect the life table of an organism. A species' life history is genetically determined and shaped by the environment and natural selection. Studying life histories can help us understand larger evolutionary questions, like why does biological aging, a deleterious reduction in fecundity and survival, exist?

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1: What is life history?

Life history theory

Life history theory is an analytical framework[1] designed to study the diversity of life history strategies used by different organisms throughout the world, as well as the causes and results of the variation in their life cycles.[2] It is a theory of biological evolution that seeks to explain aspects of organisms' anatomy and behavior by reference to the way that their life histories—including their reproductive development and behaviors, post-reproductive behaviors, and lifespan (length of time alive)—have been shaped by natural selection. A life history strategy is the "age- and stage-specific patterns"[2] and timing of events that make up an organism's life, such as birth, weaning, maturation, death, etc.[3] These events, notably juvenile development, age of sexual maturity, first reproduction, number of offspring and level of parental investment, senescence and death, depend on the physical and ecological environment of the organism.

The theory was developed in the 1950s[4] and is used to answer questions about topics such as organism size, age of maturation, number of offspring, life span, and many others.[5] In order to study these topics, life history strategies must be identified, and then models are constructed to study their effects. Finally, predictions about the importance and role of the strategies are made,[6] and these predictions are used to understand how evolution affects the ordering and length of life history events in an organism's life, particularly the lifespan and period of reproduction.[7] Life history theory draws on an evolutionary foundation, and studies the effects of natural selection on organisms, both throughout their lifetime and across generations.[8] It also uses measures of evolutionary fitness to determine if organisms are able to maximize or optimize this fitness,[9] by allocating resources to a range of different demands throughout the organism's life.[1] It serves as a method to investigate further the "many layers of complexity of organisms and their worlds".[10]

Organisms have evolved a great variety of life histories, from Pacific salmon, which produce thousands of eggs at one time and then die, to human beings, who produce a few offspring over the course of decades. The theory depends on principles of evolutionary biology and ecology and is widely used in other areas of science.



Figure 1.1**:** A swallowtail butterfly hatches from a chrysalis. Image: Pixabay

Life cycle

All organisms follow a specific sequence in their development,[9] beginning with gestation and ending with death, which is known as the life cycle. Events in between usually include birth, childhood, maturation, reproduction, and senescence, and together these comprise the life history strategy of that organism.[3] The major events in this life cycle are usually shaped by the demographic qualities of the organism.[2] Some are more obvious shifts than others, and may be marked by physical changes—for example, teeth erupting in young children.[8] Some events may have little variation between individuals in a species, such as length of gestation, but other events may show a lot of variation between individuals,[3] such as age at first reproduction. Life cycles can be divided into two major stages: growth and reproduction. These two cannot take place at the same time, so once reproduction has begun, growth usually ends.[9] This shift is important because it can also affect other aspects of an organism's life, such as the organization of its group or its social interactions.[8]

Each species has its own pattern and timing for these events, often known as its ontogeny, and the variety produced by this is what life history theory addresses.[12] Evolution then works upon these stages to ensure that an organism adapts to its environment.[5] For

example, a human, between being born and reaching adulthood, will pass through an assortment of life stages, which include: birth, infancy, weaning, childhood and growth, adolescence, sexual maturation, and reproduction.[3][12] All of these are defined in a specific biological way, which is not necessarily the same as the way that they are commonly used.[12] In life history theory, evolution works on the life stages of particular species (e.g., length of juvenile period) but is also discussed for a single organism's functional, lifetime adaptation. In both cases, researchers assume adaptation—processes that establish fitness.[5]

Traits

There are at least seven traits that are traditionally recognized as important in life history theory.[4] The trait that is seen as the most important for any given organism is the one where a change in that trait creates the most significant difference in that organism's level of fitness. In this sense, an organism's fitness is determined by its changing life history traits.[6] The way in which evolutionary forces act on these life history traits serves to limit the genetic variability and heritability of the life history strategies, [4] although there are still large varieties that exist in the world.

Commonly studied life history traits:

1. size at birth
2. growth pattern
3. age and size at maturity
4. number, size, and sex ratio of offspring
5. age- and size-specific reproductive investments
6. age- and size-specific mortality schedules
7. length of life

Strategies

Combinations of these life history traits and life events create the life history strategies. As an example, Winemiller and Rose propose three types of life history strategies in the fish they study: opportunistic, periodic, and equilibrium.[13] These types of strategies are defined by the body size of the fish, age at maturation, high or low survivorship, and the type of environment they are found in. A fish with a large body size, a late age of maturation, and low survivorship, found in a seasonal environment, would be classified as having a periodic life strategy.[13] The type of behaviors taking place during life events can also define life history strategies. For example, an exploitative life history strategy would be one where an organism benefits by using more resources than others, or by taking these resources from other organisms.[14]

Ecological conditions favor organisms with certain life history strategies through natural selection and evolution, rather than organisms favoring certain strategies based on ecological conditions.

Characteristics

Life history characteristics are traits that affect the life table of an organism, and can be imagined as various investments in growth, reproduction, and survivorship. The goal of life history theory is to understand the variation in such life history strategies. This knowledge can be used to construct models to predict what kinds of traits will be favored in different environments. Without constraints, the highest fitness would belong to a Darwinian demon, a hypothetical organism for whom such trade-offs do not exist. The key to life history theory is that there are limited resources available, and focusing on only a few life history characteristics is necessary.

Examples of some major life history characteristics include:

- Age at first reproductive event
- Reproductive lifespan and aging
- Number and size of offspring

Variations in these characteristics reflect different allocations of an individual's resources (i.e., time, effort, and energy expenditure) to competing life functions. For any given individual, available resources in any particular environment are finite. Time, effort, and energy used for one purpose diminishes the time, effort, and energy available for another.

For example, birds with larger broods are unable to afford more prominent secondary sexual characteristics.[15] Life history characteristics will, in some cases, change according to the population density, since genotypes with the highest fitness at high

population densities will not have the highest fitness at low population densities.[16] Other conditions, such as the stability of the environment, will lead to selection for certain life history traits. Experiments have found that unstable environments select for flies with both shorter lifespans and higher fecundity—in unreliable conditions, it is better for an organism to breed early and abundantly than waste resources promoting its own survival.[17]

Reproductive value and costs of reproduction

Reproductive value models the tradeoffs between reproduction, growth, and survivorship. An organism's reproductive value (RV) is defined as its expected contribution to the population through both current and future reproduction:[19]

RV = Current Reproduction + Residual Reproductive Value (RRV)

The residual reproductive value represents an organism's future reproduction through its investment in growth and survivorship. The cost of reproduction hypothesis[20] predicts that higher investment in current reproduction hinders growth and survivorship and reduces future reproduction, while investments in growth will pay off with higher fecundity (number of offspring produced) and reproductive episodes in the future. This cost-of-reproduction tradeoff influences major life history characteristics. For example, a 2009 study by Creighton et al. on burying beetles provided support for the costs of reproduction.[21] The study found that beetles that had allocated too many resources to current reproduction also had the shortest lifespans. In their lifetimes, they also had the fewest reproductive events and offspring, reflecting how over-investment in current reproduction lowers residual reproductive value.

The related terminal investment hypothesis describes a shift to current reproduction with higher age. At early ages, RRV is typically high, and organisms should invest in growth to increase reproduction at a later age. As organisms age, this investment in growth gradually increases current reproduction. However, when an organism grows old and begins losing physiological function, mortality increases while fecundity decreases. This senescence shifts the reproduction tradeoff towards current reproduction: the effects of aging and higher risk of death make current reproduction more favorable. The burying beetle study also supported the terminal investment hypothesis: the authors found beetles that bred later in life also had increased brood sizes, reflecting greater investment in those reproductive events.[22]

r/K selection theory

For more information on r/K selection see the Population Ecology chapter.

The selection pressures that determine the reproductive strategy, and therefore much of the life history, of an organism can be understood in terms of r/K selection theory. The central trade-off to life history theory is the number of offspring vs. the timing of reproduction. Organisms that are r-selected have a high growth rate (*r*) and tend to produce a high number of offspring with minimal parental care; their lifespans also tend to be shorter. *r*-selected organisms are suited to life in an unstable environment, because they reproduce early and abundantly and allow for a low survival rate of offspring. *K*-selected organisms subsist near the carrying capacity of their environment (*K*), produce a relatively low number of offspring over a longer span of time, and have high parental investment. They are more suited to life in a stable environment in which they can rely on a long lifespan and a low mortality rate that will allow them to reproduce multiple times with a high offspring survival rate.[23]

Some organisms that are very *r*-selected are **semelparous**, only reproducing once before they die. Semelparous organisms may be short-lived, like annual crops. However, some semelparous organisms are relatively long-lived, such as the African flowering plant *Lobelia telekii* which spends up to several decades growing an inflorescence that blooms only once before the plant dies,[24] or the periodical cicada which spends 17 years as a larva before emerging as an adult. Organisms with longer lifespans are usually **iteroparous**, reproducing more than once in a lifetime. However, iteroparous organisms can be more *r*-selected than *K*-selected, such as a sparrow, which gives birth to several chicks per year but lives only a few years, as compared to a wandering albatross, which first reproduces at ten years old and breeds every other year during its 40-year lifespan.[25]

***r*-selected organisms usually:**

- mature rapidly and have an early age of first reproduction
- have a relatively short lifespan
- have a large number of offspring at a time, and few reproductive events, or are semelparous
- have a high mortality rate and a low offspring survival rate

- have minimal parental care/investment

***K*-selected organisms usually:**

- mature more slowly and have a later age of first reproduction
- have a longer lifespan
- have few offspring at a time and more reproductive events spread out over a longer span of time
- have a low mortality rate and a high offspring survival rate
- have high parental investment



Figure 1.2**:** A litter of mice with their mother. The reproduction of mice follows an *r*-selection strategy, with many offspring, short gestation, less parental care, and a short time until sexual maturity Image: Seweryn Olkowicz

Trade-offs

An essential component of studying life history strategies is identifying the **trade-offs**[26] that take place for any given organism. Energy use in life history strategies is regulated by thermodynamics and the conservation of energy,[3] and the "inherent scarcity of resources",[9] so not all traits or tasks can be invested in at the same time. Thus, organisms must choose between tasks, such as growth, reproduction, and survival,[9] prioritizing some and not others. For example, there is a trade-off between maximizing body size and maximizing lifespan, and between maximizing offspring size and maximizing offspring number.[5][6] This is also sometimes seen as a choice between quantity and quality of offspring.[7] These choices are the trade-offs that life history theory studies.

One significant trade-off is between somatic effort (towards growth and maintenance of the body) and reproductive effort (towards producing offspring).[7][9] Since an organism can't put energy towards doing these simultaneously, many organisms have a period where energy is put just toward growth, followed by a period where energy is focused on reproduction, creating a separation of the two in the life cycle.[3] Thus, the end of the period of growth marks the beginning of the period of reproduction. Another fundamental trade-off associated with reproduction is between mating effort and parenting effort. If an organism is focused on raising its offspring, it cannot devote that energy to pursuing a mate.[9]

An important trade-off in the dedication of resources to breeding has to do with predation risk: organisms that have to deal with an increased risk of predation often invest less in breeding. This is because it is not worth as much to invest a lot in breeding when the benefit of such investment is uncertain.[27]

These trade-offs, once identified, can then be put into models that estimate their effects on different life history strategies and answer questions about the selection pressures that exist on different life events.[7] Over time, there has been a shift in how these models are constructed. Instead of focusing on one trait and looking at how it changed, scientists are looking at these trade-offs as part of a larger system, with complex inputs and outcomes.[6]

The idea of **constraints** is closely linked to the idea of trade-offs discussed above. Because organisms have a finite amount of energy, the process of trade-offs acts as a natural limit on the organism's adaptations and potential for fitness. These limits can be physical, developmental, or historical, and they are imposed by the existing traits of the organism.[2]

Populations can adapt and thereby achieve an **"optimal" life history strategy** that allows the highest level of fitness possible (fitness maximization). There are several methods from which to approach the study of optimality, including energetic and demographic. Achieving optimal fitness also encompasses multiple generations, because the optimal use of energy includes both

the parents and the offspring. For example, "optimal investment in offspring is where the decrease in total number of offspring is equaled by the increase of the number who survive".[7] Optimality is important for the study of life history theory because it serves as the basis for many of the models used, which work from the assumption that natural selection, as it works on a life history traits, is moving towards the most optimal group of traits and use of energy.[6] This base assumption, that over the course of its life span an organism is aiming for optimal energy use,[7] then allows scientists to test other predictions. However, actually gaining this optimal life history strategy cannot be guaranteed for any organism.[6]

An organism's **allocation of resources** ties into several other important concepts, such as trade-offs and optimality. The best possible allocation of resources is what allows an organism to achieve an optimal life history strategy and obtain the maximum level of fitness,[9] and making the best possible choices about how to allocate energy to various trade-offs contributes to this. The allocation of resources also plays a role in variation, because the different resource allocations by different species create the variety of life history strategies.[3]

Unpredictable environments

Many factors can determine the evolution of an organism's life history, especially the unpredictability of the environment. A very unpredictable environment—one in which resources, hazards, and competitors may fluctuate rapidly—selects for organisms that produce more offspring earlier in their lives, because it is never certain whether they will survive to reproduce again. Mortality rate may be the best indicator of a species' life history: organisms with high mortality rates—the usual result of an unpredictable environment—typically mature earlier than those species with low mortality rates, and give birth to more offspring at a time.[32] A highly unpredictable environment can also lead to plasticity, in which individual organisms can shift along the spectrum of r-selected vs. K-selected life histories to suit the environment.[33]

Evolution Connection: Energy Budgets, Reproductive Costs, and Sexual Selection in *Drosophila*

Research into how animals allocate their energy resources for growth, maintenance, and reproduction has used a variety of experimental animal models. Some of this work has been done using the common fruit fly, *Drosophila melanogaster*. Studies have shown that not only does reproduction have a cost as far as how long male fruit flies live, but also fruit flies that have already mated several times have limited sperm remaining for reproduction. Fruit flies maximize their last chances at reproduction by selecting optimal mates.

In a 1981 study, male fruit flies were placed in enclosures with either virgin or inseminated females. The males that mated with virgin females had shorter life spans than those in contact with the same number of inseminated females with which they were unable to mate. This effect occurred regardless of how large (indicative of their age) the males were. Thus, males that did not mate lived longer, allowing them more opportunities to find mates in the future.

More recent studies, performed in 2006, show how males select the female with which they will mate and how this is affected by previous matings (Figure 1.3). Males were allowed to select between smaller and larger females. Findings showed that larger females had greater fecundity, producing twice as many offspring per mating as the smaller females did. Males that had previously mated, and thus had lower supplies of sperm, were termed “resource-depleted,” while males that had not mated were termed “non-resource-depleted.” The study showed that although non-resource-depleted males preferentially mated with larger females, this selection of partners was more pronounced in the resource-depleted males. Thus, males with depleted sperm supplies, which were limited in the number of times that they could mate before they replenished their sperm supply, selected larger, more fecund females, thus maximizing their chances for offspring. This study was one of the first to show that the physiological state of the male affected its mating behavior in a way that clearly maximizes its use of limited reproductive resources.

	Ratio large/small females mated
Non sperm-depleted	8 ± 5
Sperm-depleted	15 ± 5

Figure 1.3**:** Male fruit flies that had previously mated (sperm-depleted) picked larger, more fecund females more often than those that had not mated (non-sperm-depleted). This change in behavior causes an increase in the efficiency of a limited reproductive resource: sperm.

These studies demonstrate two ways in which the energy budget is a factor in reproduction. First, energy expended on mating may reduce an animal's lifespan, but by this time they have already reproduced, so in the context of natural selection this early death is not of much evolutionary importance. Second, when resources such as sperm (and the energy needed to replenish it) are low, an organism's behavior can change to give them the best chance of passing their genes on to the next generation. These changes in behavior, so important to evolution, are studied in a discipline known as behavioral biology, or ethology, at the interface between population biology and psychology.

Adapted from Phillip G. Byrne and William R. Rice, "Evidence for adaptive male mate choice in the fruit fly *Drosophila melanogaster*," Proc Biol Sci. 273, no. 1589 (2006): 917-922, doi: 10.1098/rspb.2005.3372.

Human life history

In studying humans, life history theory is used in many ways, including in biology, psychology, economics, anthropology, and other fields.[9][34][35] For humans, life history strategies include all the usual factors—trade-offs, constraints, reproductive effort, etc.—but also includes a culture factor that allows them to solve problems through cultural means in addition to through adaptation.[5] Humans also have unique traits that make them stand out from other organisms, such as a large brain, later maturity and age of first reproduction,[7] a long lifespan,[7][36] and a high level of reproduction, often supported by fathers and older (post-menopausal) relatives.[36][37][38] There are a variety of possible explanations for these unique traits. For example, a long juvenile period may have been adapted to support a period of learning the skills needed for successful hunting and foraging.[7][36] This period of learning may also explain the longer lifespan, as a longer amount of time over which to use those skills makes the period needed to acquire them worth it.[8][36] Cooperative breeding and the "grandmother hypothesis" have been proposed as the reasons that humans continue to live for many years after they are no longer capable of reproducing.[7][38] The large brain allows for a greater learning capacity, and the ability to engage in new behaviors and create new things.[7] The change in brain size may have been the result of a dietary shift—towards higher quality and difficult to obtain food sources[36]—or may have been driven by the social requirements of group living, which promoted sharing and provisioning.[8] Research has also indicated that humans may pursue different reproductive strategies.[39][40][41]

Survivorship Curves

Another tool used by population ecologists is a survivorship curve, which is a graph of the number of individuals surviving at each age interval plotted versus time (usually with data compiled from a life table). These curves allow us to compare the life histories of different populations (Figure 1.4). Humans and most primates exhibit a **Type I survivorship curve** because a high percentage of offspring survive their early and middle years—death occurs predominantly in older individuals. These types of species usually have small numbers of offspring at one time, and they give a high amount of parental care to them to ensure their survival. Birds are an example of an intermediate or **Type II survivorship curve** because birds die more or less equally at each age interval. These organisms also may have relatively few offspring and provide significant parental care. Trees, marine invertebrates, and most fishes exhibit a **Type III survivorship curve** because very few of these organisms survive their younger years; however, those that make it to an old age are more likely to survive for a relatively long period of time. Organisms in this category usually have a very large number of offspring, but once they are born, little parental care is provided. Thus these offspring are "on their own" and vulnerable to predation, but their sheer numbers assure the survival of enough individuals to perpetuate the species.

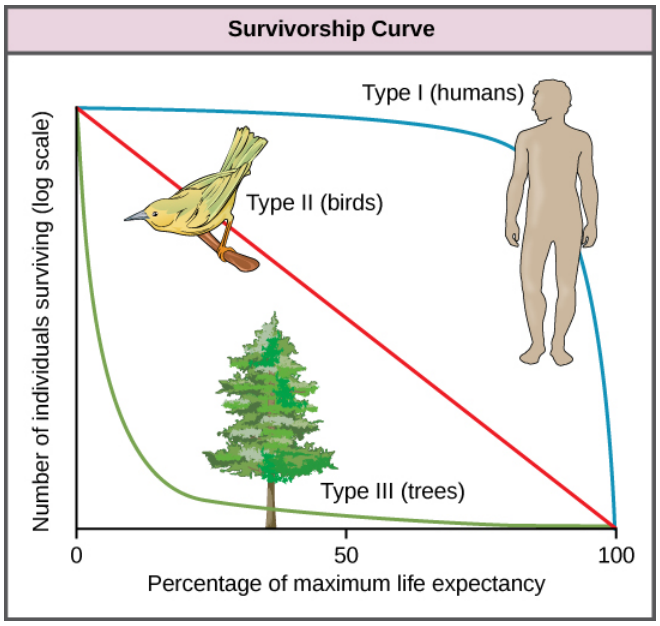


Figure 1.4**:** Survivorship curves show the distribution of individuals in a population according to age. Humans and most mammals have a Type I survivorship curve because death primarily occurs in the older years. Birds have a Type II survivorship curve, as death at any age is equally probable. Trees have a Type III survivorship curve because very few survive the younger years, but after a certain age, individuals are much more likely to survive.

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1.1: Scientist Spotlight - Erin Satterthwaite

Relative to the offspring of other species, humans enter the world utterly defenseless. Emerging from a 9-month gestation period, we arrive completely dependent upon our caregivers. In contrast, newly hatched (or birthed) marine larvae are amazingly independent. Swimming, something humans may never learn in their lifetime, is an elementary skill required for the survival of mobile *and* sessile marine organisms.

Sessile means, “permanently attached or established : not free to move about” (Merriam-Webster n.d.). Something does not add up here. Sessile organisms move? Yes, when they are in the midst of the larval life stage. Both sessile and mobile marine animals, including species of fish, sponge, crab, sea star, worm, and snail experience this microscopic phase. According to Dr. Erin Satterthwaite, a marine ecologist with California Sea Grant at Scripps Institution of Oceanography , dispersal of marine young “is one of the primary determinants of recruitment of new individuals into populations and can be an important driver of population dynamics,” (Drake et al. 2018). In other words, larval movement affects how larvae settle into new populations. In turn, population size and structure influence how those populations interact with the environment and the rest of their community (Khan Academy n.d.). Dr. Satterthwaite and her colleagues found that when larvae swam toward shore (as opposed to not swimming toward shore), there was “a substantial increase in nearshore larval supply,” which meant that there would be more young available to settle into suitable habitat (Drake et al. 2018). This demonstrated that larval behavior may be an important factor shaping marine population dynamics. Overall, in order to understand and conserve marine animals, we need to better understand where they are born from, where they end up, and how they got there.

Dr. Satterthwaite’s favorite part of being a marine ecologist has been exploring nature and sharing its wonders with others. As a first-generation college and graduate student, her “path has been a winding journey,” and she “has had to rely on others for support and guidance.” For Dr. Satterthwaite, it has been this sense of community and relationships she has built along the way that has been the best part of her career.



Figure 1.1.1: A photo of Dr. Erin Satterthwaite contributed to Project Biodiversify by Dr. Satterthwaite.

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Scientist Spotlight inspiration from Project Biodiversify

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2: Life History Evolution

The content for this subtopic is found in an external page. Please click the link below to access this information.

Life History Evolution

Fabian, D. & Flatt, T. (2012). Life History Evolution. *Nature Education Knowledge*, *3*(10):24

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3: The Evolution of Aging

The Evolution of Aging

Senescence or **biological aging** is the gradual deterioration of functional characteristics in living organisms. The word *senescence* can refer to either cellular senescence or to senescence of the whole organism. Organismal senescence involves an increase in death rates and/or a decrease in fecundity with increasing age, at least in the latter part of an organism's life cycle. Environmental factors may affect aging - for example, overexposure to ultraviolet radiation accelerates skin aging. Different parts of the body may age at different rates. Two organisms of the same species can also age at different rates, making biological aging and chronological aging distinct concepts.

The occurrence of aging in nature poses an evolutionary puzzle: why would such a deleterious, maladaptive process evolve? This puzzle is deepened by the fact that aging is apparently neither inevitable nor universal: germ lines and several organisms do not exhibit senescent decline.

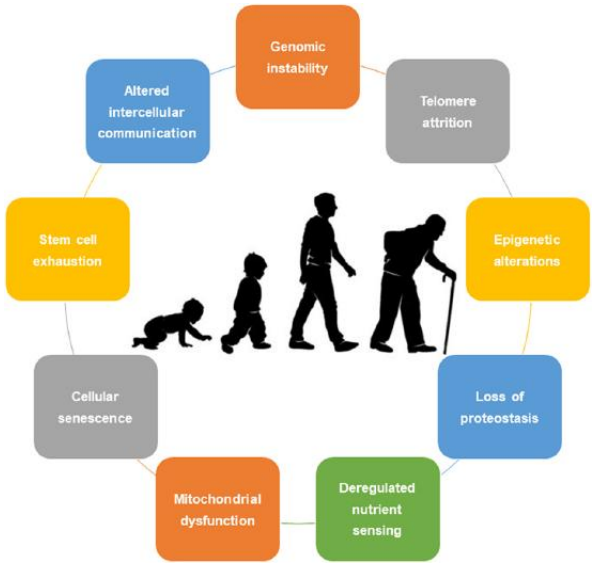


Figure 3.1**:** The nine hallmarks of aging that are common among organisms: genomic instability, telomere attrition, epigenetic alterations, loss of proteostasis, deregulated nutrient sensing, mitochondrial dysfunction, cellular senescence, stem cell exhaustion, and altered intercellular communication. *Source: Rebelo-Marques, De Sousa Lages, Andrade, Ribeiro, Mota-Pinto, Carrilho and Espregueira-Mendes - https://www.frontiersin.org/articles/10.3389/fendo.2018.00258/full.*

Is aging universal? Diverse patterns of senescence among species

Classic theories of aging pertain mainly to relatively short-lived species with increasing mortality and decreasing fertility after maturity, but patterns of aging—including reproductive senescence—are very diverse (Finch 1990, Shefferson et al. 2017, Comfort 1956, Jones et al. 2014, Baudisch et al. 2013, Garcia et al. 2011, Schaible et al. 2015, Ruby et al. 2018, Lemaitre & Gaillard 2017). In particular, although many species do age, some appear to show 'negligible' senescence (i.e., only weak or no signs of aging with advancing age; Finch 1990, Shefferson et al. 2017, Finch & Austad 2001, Finch 2009, Finch 1998), whereas others could—at least theoretically—exhibit 'negative' senescence (i.e., physiological improvement with age; Vaupel et al. 2004). In freshwater polyps of the genus *Hydra* (Figure 3.2), for instance, survival and fertility do not decline with age (Schaible et al. 2015). Similarly, many plants (e.g., ~93% of angiosperms) show no signs of aging (Salguero-Gómez et al. 2013, Baudisch et al. 2013); some trees, for example, live thousands of years (Figure 3.2). However, a caveat is that aging might in many cases exist but not be detectable because the studied individuals were not old enough (Peron et al. 2010); for example, a recent study of turtles—typically thought of as exhibiting strongly 'negligible' senescence—has shown that reproduction and survival do in fact decline with age, contrary to previous expectations. Many organisms, such as numerous invertebrates and fish, start to reproduce before they are fully grown.

Increasing body size can then lead to increased fecundity and also to protection against size-specific predators and other sources of mortality. Under these circumstances, the force of natural selection can increase over part of adult life, because the reproductive value of the organism increases (Baudisch 2008, Baudisch 2005, Charlesworth 1994, Partridge & Barton 1996). Non- or slow-aging species, including some animals (e.g., basal metazoans such as *Hydra* and sea anemones) and most higher plants, are characterized by modular organization, indeterminate (including clonal) growth, and the capacity to regenerate due to stem cell activity; often such organisms start to reproduce before they have finished growing, or they can grow indefinitely (Munné-Bosch 2015, Petralia et al. 2014, Bythell et al. 2017). Some clones of grasses, for example, have been estimated to become 15,000 years old (Noodén 1988). In addition, unlike the standard laboratory model organisms, which set aside and sequestrate their germline early in development, in organisms such as *Hydra* and higher plants the cells that will become the germline are only identified during adulthood, and these organisms therefore maintain cell lineages with high regenerative potential. Thus, the force of natural selection does not always decline monotonically with age (Baudisch 2008, Munné-Bosch 2015, Shefferson et al. 2017 Baudisch 2005, Charlesworth 1994).

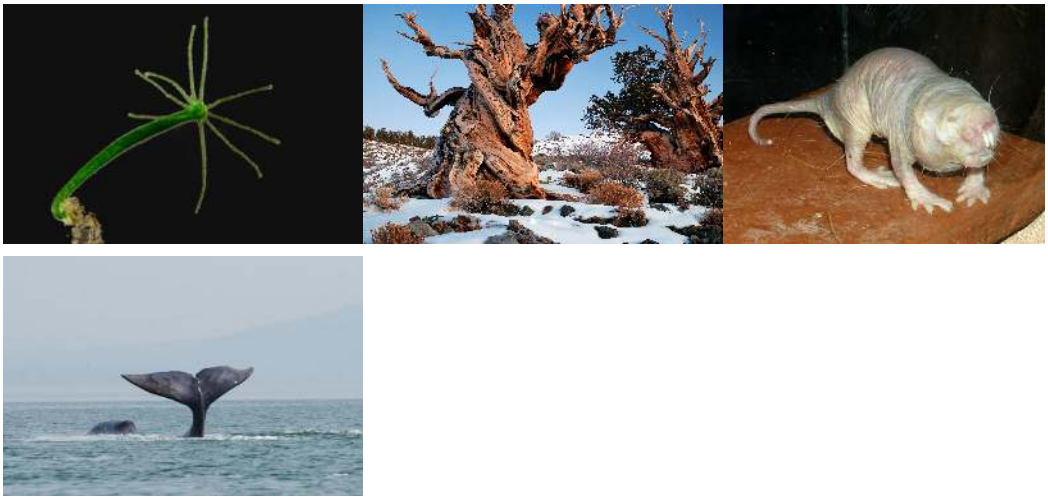


Figure 3.2**:** Long-lived organisms; many organisms age very slowly, if at all. Left: the freshwater polyp *Hydra* is potentially immortal ("Hydra" by Frank Fox is licensed under CC BY-SA 3.0). Second from left: some trees like this bristlecone pine (*Pinus longaeva*) live for thousands of years ("Gnarly" by Rick Goldwaser is licensed under CC BY 2.0). Third from left: in the naked mole-rat (*Heterocephalus glaber*) mortality does not increase with age ("Nacktmull" by Roman Klementschitz is licensed under CC BY-SA 3.0). Right: the bowhead whale (*Balaena mysticetus*) is the longest-lived mammal, with an estimated maximum life span of 211 years ("A bowhead whale" by Olga Shpak is licensed under CC BY-SA 3.0).

Hypotheses of aging

More than 300 different hypotheses have been posited to explain the nature and causes of aging. Aging hypotheses fall into two broad categories, evolutionary hypotheses of aging and mechanistic hypotheses of aging. Evolutionary hypotheses of aging primarily explain why aging happens, but do not concern themselves with how (the molecular mechanism(s)). All evolutionary hypotheses of aging rest on the basic mechanisms that the force of natural selection declines with age. Mechanistic hypotheses of aging can be divided into hypotheses that propose aging is programmed (i.e., aging follows a biological timetable), and damage accumulation hypotheses (i.e., those that propose aging to be caused by specific molecular changes occurring over time).

Evolutionary aging hypotheses

Antagonistic pleiotropy

One hypothesis proposed by George C. Williams involves **antagonistic pleiotropy**. Pleiotropy occurs when a single gene has two or more apparently unrelated effects. The idea of antagonistic pleiotropy is that one gene can positively affect a fitness related trait early in life, but can also have negative effects later in life and thus contribute to senescence. Because many more individuals are alive at young ages than at old ages, even small positive effects early can be strongly selected for, and large negative effects later

may be very weakly selected against. Williams suggested the following example: Perhaps a gene codes for calcium deposition in bones, which promotes juvenile survival and will therefore be favored by natural selection; however, this same gene promotes calcium deposition in the arteries, causing negative atherosclerotic effects in old age. Thus, harmful biological changes in old age may result from selection for pleiotropic genes that are beneficial early in life but harmful later on. In this case, selection pressure is relatively high when Fisher's reproductive value is high and relatively low when Fisher's reproductive value is low.

Cancer versus cellular senescence trade-off

Senescent cells within a multicellular organism can be purged by competition between cells, but this increases the risk of cancer. This leads to an inescapable dilemma between two possibilities—the accumulation of physiologically useless senescent cells, and cancer—both of which lead to increasing rates of mortality with age.

Disposable soma

The **disposable soma hypothesis** of aging was proposed by Thomas Kirkwood in 1977. The hypothesis suggests that aging occurs due to a strategy in which an individual only invests in maintenance of the soma for as long as it has a realistic chance of survival. A species that uses resources more efficiently will live longer, and therefore be able to pass on genetic information to the next generation. The demands of reproduction are high, so less effort is invested in repair and maintenance of somatic cells, compared to germline cells, in order to focus on reproduction and species survival.

Damage accumulation hypotheses

The free radical hypothesis

One of the most prominent hypotheses of aging was first proposed by Harman in 1956. It posits that free radicals produced by dissolved oxygen, radiation, cellular respiration and other sources cause damage to the molecular machines in the cell and gradually wear them down. This is also known as oxidative stress. Under normal aerobic conditions, approximately 4% of the oxygen metabolized by mitochondria is converted to superoxide ion, which can subsequently be converted to hydrogen peroxide, hydroxyl radical and eventually other reactive species including other peroxides and singlet oxygen, which can, in turn, generate free radicals capable of damaging structural proteins and DNA.

There is substantial evidence to back up this theory. Old animals have larger amounts of oxidized proteins, DNA and lipids than their younger counterparts.

Chemical damage

One of the earliest aging hypotheses was the *Rate of Living Hypothesis* described by Raymond Pearl in 1928, which states that fast basal metabolic rate corresponds to shortened maximum life span.

While there may be some validity to the idea that for various types of specific damage detailed below that are byproducts of metabolism, all other things being equal, a fast metabolism may reduce life span, in general this hypothesis does not adequately explain the differences in life span either within, or between, species. Calorically restricted animals process as much, or more, calories per gram of body mass, as their *ad libitum* fed counterparts, yet exhibit substantially longer life spans. Similarly, metabolic rate is a poor predictor of life span for birds, bats and other species that, it is presumed, have reduced mortality from predation, and therefore have evolved long life spans even in the presence of very high metabolic rates. In a 2007 analysis it was shown that, when modern statistical methods for correcting for the effects of body size and phylogeny are employed, metabolic rate does not correlate with longevity in mammals or birds.

With respect to specific types of chemical damage caused by metabolism, it is suggested that damage to structural proteins or DNA caused by ubiquitous chemical agents in the body such as oxygen and sugars, are in part responsible for aging. The damage can include breakage of biopolymer chains, cross-linking of biopolymers, or chemical attachment of unnatural substituents to biopolymers. Sugars such as glucose and fructose can react with certain amino acids such as lysine and arginine and certain DNA bases such as guanine to produce sugar adducts, in a process called *glycation*. These adducts can further rearrange to form reactive species, which can then cross-link the structural proteins or DNA to similar biopolymers or other biomolecules such as non-structural proteins. There is evidence that sugar damage is linked to oxidant damage in a process termed *glycoxidation*.

Mutation accumulation

Natural selection can support lethal and harmful alleles, if their effects are felt after reproduction. The geneticist J. B. S. Haldane wondered why the dominant mutation that causes Huntington's disease remained in the population, and why natural selection had not eliminated it. The onset of this neurological disease is (on average) at age 45 and is invariably fatal within 10–20 years. Haldane assumed that, in human prehistory, few survived until age 45. Since few were alive at older ages and their contribution to the next generation was therefore small relative to the large cohorts of younger age groups, the force of selection against such late-acting deleterious mutations was correspondingly small. Therefore, a genetic load of late-acting deleterious mutations could be substantial at mutation–selection balance. This concept came to be known as the **selection shadow** (Figure 3.3).

Peter Medawar formalized this observation in his mutation accumulation hypothesis of aging. "The force of natural selection weakens with increasing age—even in a theoretically immortal population, provided only that it is exposed to real hazards of mortality. If a genetic disaster... happens late enough in individual life, its consequences may be completely unimportant".

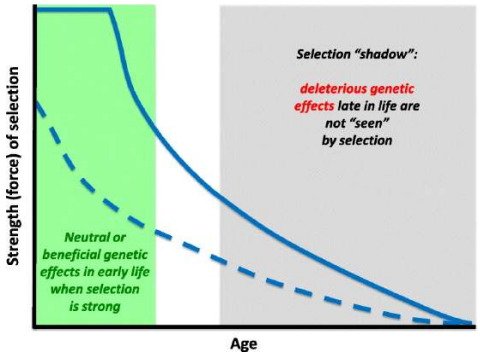


Figure 3.3**:** The declining force of selection. The strength ('force') of selection measures how strongly natural selection acts on changes in survival and/or fecundity. Often, but not always, the force of selection declines with age. If this is the case, then alleles with neutral effects on fitness early in life but with deleterious effects late in life can accumulate in a population, unchecked by selection (mutation accumulation). Similarly, alleles with positive effects on fitness components early in life can be selectively favored even if they have negative effects late in life (antagonistic pleiotropy). The late-life negative effects in the 'selection shadow' cannot be effectively eliminated by selection, leading to senescence. While the force acting on survival (solid line) only starts to decrease with age after the onset of reproduction, the strength of selection on fecundity (dashed line) can increase or decrease before the onset of reproduction. *Source: Flatt and Partridge,* https://doi.org/10.1186/s12915-018-0562-z.

Trade-offs with life span are pervasive but can be uncoupled

Studies of natural populations have also found support for phenotypic trade-offs consistent with the notion of antagonistic pleiotropy / disposable soma (Nussey et al. 2013, Peron et al. 2010). In bats, for example, species that produce more offspring are shorter-lived than those that produce fewer offspring (Kim et al. 2011). Similarly, a recent review of 26 studies of free-ranging populations of 24 vertebrate species (birds, mammals, reptiles) has identified clear-cut trade-offs between early and late fitness components (Lemaitre et al. 2015), and data in humans have unraveled a genetically based trade-off between reproduction and life span (Wang et al. 2013). Trade-offs thus seem to be pervasive: high resource allocation to growth or reproduction early in life is often associated with earlier or more rapid aging. However, there is also growing evidence that trade-offs between life span and other fitness components are context-dependent and can be 'uncoupled', as is observed in some long-lived *C. elegans* or *Drosophila* mutants (Flatt & Schmidt 2009, Flatt 2011, Rodrigues & Flatt 2016, Flatt & Heyland 2011), or upon manipulation of specific dietary amino acids in flies (Grandison et al. 2009, Selman et al. 2008; see below), without any apparent fitness costs of longevity. In these cases, a likely explanation is the artificially benign laboratory environment occupied by these organisms, which may allow them to realize their physiologically maximal possible investments into both survival and reproduction.

The most famous example of an 'uncoupling' of the fecundity–longevity trade-off is seen in eusocial insects (i.e., ants, bees, termites). In many ants, for example, queens are extraordinarily long-lived and highly fertile as compared to the short-lived and

sterile workers (Rodrigues & Flatt 2016, Keller & Genoud 1997, Keller & Jemielity 2006, Kuhn & Korb 2016, Heinze & Schrempf 2008, Schrempf et al. 2017, von Wyschetzki et al. 2015, Hartmann & Heinze 2003, Kramer et al. 2015), even though within the worker caste reproductive costs have been found among fertile bumblebee workers (Blacher et al. 2017). On the other hand, in naked mole rats, which are also eusocial, queens and workers have approximately equivalent life spans but workers do not reproduce while queens can produce up to 900 pups (Buffenstein & Jarvis 2002). How can social insect queens (or kings in termites) escape this trade-off? Surprisingly little formal analysis of this problem exists; the standard explanation that has been put forward is that queens and kings live much longer because they are shielded from extrinsic mortality by the workers (Keller & Genoud 1997, Heinze & Schrempf 2008). In addition, queens or kings may defy the fecundity–longevity trade-off because of trade-offs at the colony level (Kramer et al. 2016), with resources provided by workers freeing them from individual-level trade-offs; at the colony level, queens and kings might be viewed, metaphorically, as representing the 'immortal germline', whereas workers can be seen as representing the 'disposable soma' (Kramer & Schaible 2013). Classic theories of aging may also not fully apply to eusocial insects (Kramer et al. 2016): their populations exhibit not only age structure but also strong social structure and division of labor. Since in such a situation survival is not only age- but also state-dependent, the force of selection does not necessarily decline with age (Williams & Day 2003). More theoretical work on aging in eusocial insects is warranted, especially the development of class-structured inclusive fitness (kin selection) models (Rodrigues & Flatt 2016, Kramer et al. 2016, Kramer & Schaible 2013, Bourke 2007).

An important insight into the likely explanation for the 'breaking' or 'uncoupling' of trade-offs comes from the different outcomes of attempts to measure reproductive costs by looking at natural correlations across individuals as opposed to experimental manipulation of reproductive rate. Generally, *across* individuals in natural populations, there is a positive phenotypic correlation between fecundity and life span. However, the causal connection between the two traits may be the opposite, as experimental manipulations of, for instance, increasing clutch size in birds, often lead to reduced future fecundity or survival (Partridge 1992). This difference occurs because the *individual variation* in condition and circumstances may obscure the underlying cost of reproduction: healthy individuals in a rich environment may have high fecundity and life span despite the cost of reproduction, which is only revealed by experimental manipulations. This concept has been termed the '**big house, big car effect**' (van Noordwijk & de Jong 1986). This underlying cost of reproduction may then constrain the combinations of life history traits that can evolve (van Noordwijk & de Jong 1986, Metcalf 2016). Organisms that live in an environment that is beneficial for development may indeed not experience costs of reproduction (van Noordwijk & de Jong 1986, Metcalf 2016), as often seems to be the case in laboratory animals (Klepsatel et al. 2013). In addition, positive correlations between fitness-related traits can also be caused by mutational variation in recessive deleterious effects (Charlesworth 1990). This arises because such deleterious mutations can have negative pleiotropic effects on two or more traits but the extent of these negative effects varies genetically among individuals.

Definition: The big house, big car effect

The *big house, big car effect* says that individuals differ in the amount of resources (energy, time, or space) they can allocate to competing demands. For example, in humans, each of us has a limited amount of monetary resources. If we were forced to choose between spending our money on a nice house or a nice car (an allocation trade-off), most of us would end up with either a nice house or a nice car, but some people are super wealthy and can afford *both* a big house and a nice car. If we are only looking *across* individuals and not accounting for the amount of resources each has accumulated, we often see patterns like this, which suggest an uncoupling of trade-offs. But because individuals differ in their available resources, this observation is not an accurate representation of the true trade-off that is being experience by each individual at the *within-individual level*.

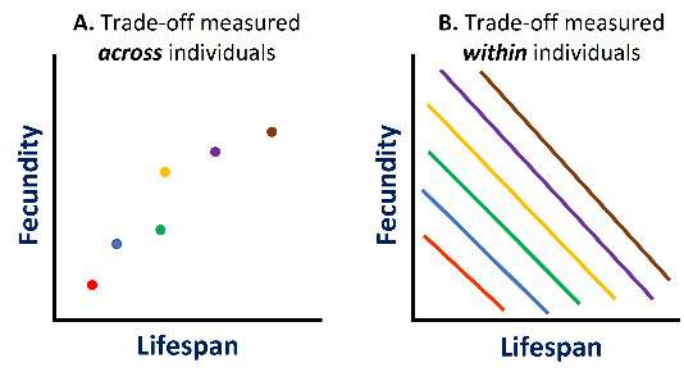


Figure 3.4**:** The 'big house, big car effect' states that individuals differ in the amount of resources they can allocate to competing demands, and thus if we were to correlate life history traits across individuals (A), we can observe an uncoupling of the trade-off. However, because individuals differ in their available resources, this observation is not an accurate representation of the true trade-off that is being experience by each individual at the within-individual level (B). Each color of dot or line represents a different individual with a different amount of resources. *Source: Dan Wetzel.*

The evolution of aging in humans

Human life expectancy worldwide has increased dramatically. During the ~300,000 generations since the divergence from our most recent common ancestor with the great apes, life span evolved to double its previous value (Finch 2010). In the last ~200 years there has been a further substantial increase, on average about 2.5 years per decade, attributable to environmental changes, including improved food, water, hygiene, and living conditions, reduced impact of infectious disease with immunization and antibiotics, and improved medical care at all ages (Vaupel et al. 1998, Wilmoth 2000, Oeppen & Vaupel 2002, Vaupel 2010). Many modern humans inhabit a very different environment from that in which their life history evolved, with both protection from many of its dangers, such as predators, infectious diseases, and harsh physical conditions, and freedom from the need to forage extensively to avoid starvation (Finch 2010). As a result, most people are now living long beyond the ages at which most would have been dead in the past. Natural selection has therefore not had an opportunity to maintain evolutionary fitness at older ages.

In humans, where age-related changes are particularly well documented, aging has proved to be a complex process of functional decline and accumulation of diverse pathologies in different tissues (Lopez-Otin et al. 2013, Kirkwood et al. 1999). Williams predicted in 1957 that aging is likely to be a genetically complex trait, and different lineages and taxa might well exhibit different proximate mechanisms of senescence. Indeed, natural variation in the rate of aging is likely influenced by many genes (Burke et al. 2014, Highfill et al. 2016, Ivanov et al. 2015), since survival and reproduction between them harness the activity of much of the genome.



Figure 3.5**:** Aging in humans. *Source: RODNAE Productions and Andrea Piacquadio.*

Prevention of late-life morbidity in humans ideally would involve interventions that could be started at the earliest in middle age. Pharmacological prevention of cardiovascular disease, with statins and blood pressure lowerers, is already routine in clinical practice (Sundstrom et al. 2018). Unsurprisingly, many of the proteins that have turned out to be important in aging also play prominent roles in the etiology of age-related diseases, and are already the targets of licensed drugs. Consideration is hence starting to be given to widening the preventative, pharmacological approach, for instance by repurposing drugs that are used to treat cancer, prevent rejection of transplanted organs, and diabetes because they have been found to extend life span in model organisms (Blenis 2017, Mannick et al. 2014, Barzilai et al. 2016, Johnson & Kaeberlein 2016). Other possible approaches to emerge from experimental work with animals include removal of damaging senescent cells that accumulate during aging (Childs et al. 2015, Rando & Chang 2012), use of factors from young blood that restore the age-related loss of function of stem cells or synapses between nerve cells in the brain (Rando & Chang 2012, Mair & Dillin 2008), and alteration of the composition of the microorganisms in the gut to a younger profile (Clark & Walker 2018, Kundu et al. 2017, Schmidt et al. 2018), which has already been shown to extend life span in the turquoise killifish (Smith et al. 2017).

However, despite the considerable promise of these approaches, the extent to which they can yield health benefits free of side effects needs detailed study, since they could pose some new challenges for an aged system. For instance, removal of senescent cells, or restoration of stem cell function, could be beneficial in the short term, but in the longer term could lead to stem cell exhaustion and tissue dysfunction.

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4: Semelparity versus Iteroparity

Semelparity versus Iteroparity

Semelparity and **iteroparity** are two contrasting reproductive strategies available to living organisms. A species is considered **semelparous** if it is characterized by a single reproductive episode before death, and **iteroparous** if it is characterized by multiple reproductive cycles over the course of its lifetime.

In truly semelparous species, death after reproduction is part of an overall strategy that includes putting all available resources into maximizing reproduction, at the expense of future life. In any iteroparous population there will be some individuals who die between their first and second reproductive episodes, but unless this is part of a syndrome of programmed death after reproduction, this would not be called semelparity.

This distinction is also related to the difference between annual and perennial plants. An annual is a plant that completes its life cycle in a single season, and is usually semelparous. Perennials live for more than one season and are usually (but not always) iteroparous (Gotelli, 2008).

Semelparity and iteroparity are not, strictly speaking, alternative strategies, but extremes along a continuum of possible modes of reproduction. Many organisms considered to be semelparous can, under certain conditions, separate their single bout of reproduction into two or more episodes (Futami & Akimoto, 2005; Hughes & Simons, 2014).

Semelparity

The word semelparity was coined by evolutionary biologist Lamont Cole, and comes from the Latin *semel* 'once, a single time' and *pario* 'to beget' (Cole, 1954). This differs from iteroparity in that iteroparous species are able to have multiple reproductive cycles and therefore can mate more than once in their lifetime. Semelparity is also known as "big bang" reproduction, since the single reproductive event of semelparous organisms is usually large as well as fatal (Ricklefs & Miller, 1999). A classic example of a semelparous organism is Pacific salmon (*Oncorhynchus* spp.), which lives for many years in the ocean before swimming to the freshwater stream of its birth, spawning, and dying. Other semelparous animals include many insects, including some species of butterflies, cicadas, and mayflies, many arachnids, and some molluscs such as some species of squid and octopus. Annual plants, including all grain crops and most domestic vegetables, are semelparous. Long-lived semelparous plants include century plant (agave), *Lobelia telekii*, and some species of bamboo.



Figure 4.1**:** Many Pacific salmon, like this sockeye salmon (*Oncorhynchus nerka*) are semelparous and only reproduce once in their lifetime. *Source: Milton Love, Marine Science Institute, available in the public domain.*

This form of lifestyle is consistent with **r-selected strategies** as many offspring are produced and there is low parental input, as one or both parents die after mating. All of the male's energy is diverting into mating and the immune system is repressed. High levels of corticosteroids are sustained over long periods of time. This triggers immune and inflammatory system failure and gastrointestinal hemorrhage, which eventually leads to death.

Iteroparity

The term iteroparity comes from the Latin *itero*, to repeat, and *pario*, to beget. An example of an iteroparous organism is a human —humans are biologically capable of having offspring many times over the course of their lives. Iteroparous vertebrates include all

birds, most reptiles, virtually all mammals, and most fish. Among invertebrates, most mollusca and many insects (for example, mosquitoes and cockroaches) are iteroparous. Most perennial plants are iteroparous.



Figure 4.2**:** Most mammals, like this domestic pig are iteroparous and reproduce multiple times in their life. *Source: Scott Bauer, USDA, available in the public domain.*

Trade-offs

Within its lifetime, an organism has a limited amount of energy/resources available to it and must always partition it among various functions such as collecting food and finding a mate. Of relevance here is the trade-off between fecundity, growth, and survivorship in its life history strategy. These trade-offs come into play in the evolution of iteroparity and semelparity. It has been repeatedly demonstrated that semelparous species produce more offspring in their single fatal reproductive episode than do closely related iteroparous species in any one of theirs. However, the opportunity to reproduce more than once in a lifetime, and possibly with greater care for the development of offspring produced, can offset this strictly numerical benefit.

Models based on non-linear trade-offs

One class of models that tries to explain the differential evolution of semelparity and iteroparity examines the shape of the trade-off between offspring produced and offspring forgone (offspring that will not be produced). In economic terms, offspring produced is equivalent to a benefit function, while offspring forgone is comparable to a cost function. The reproductive effort of an organism—the proportion of energy that it puts into reproducing, as opposed to growth or survivorship—occurs at the point where the distance between offspring produced and offspring forgone is the greatest (Figure 3).

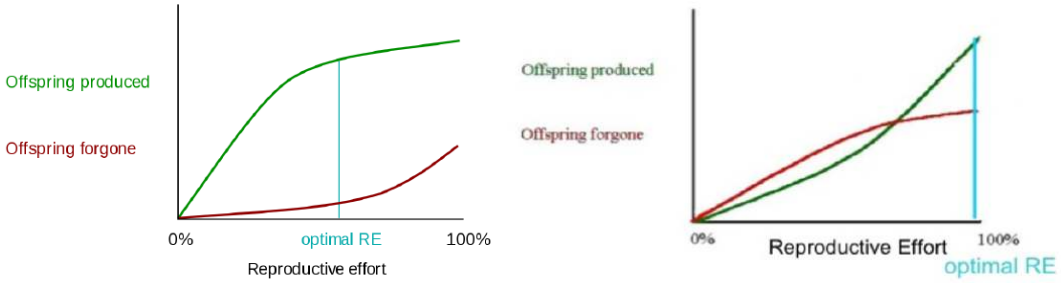


Figure 4.3**:** A visual model to explain the evolution of semelparity and iteroparity based on different cost/benefit curves. In the first graph, the marginal cost of offspring produced is decreasing (each additional offspring is less "expensive" than the average of all previous offspring) and the marginal cost of offspring forgone is increasing. In this situation, the organism only devotes a portion of its resources to reproduction, and uses the rest of its resources on growth and survivorship so that it can reproduce again in the future (Roff, 1992). However, it is also possible (second graph) for the marginal cost of offspring produced to *increase*, and for the marginal cost of offspring forgone to decrease. When this is the case, it is favorable for the organism to reproduce a single time. The organism devotes all of its resources to that one episode of reproduction, so it then dies. This mathematical/graphical model has found only limited quantitative support from nature. *Source: Paul Moorcroft, Harvard University, licensed under CC BY-SA 3.0.*

Bet-hedging models

A second set of models examines the possibility that iteroparity is a hedge against unpredictable juvenile survivorship (avoiding putting all one's eggs in one basket). Again, mathematical models have not found empirical support from real-world systems. In fact, many semelparous species live in habitats characterized by high (not low) environmental unpredictability, such as deserts and early successional habitats.

Cole's paradox and demographic models

The models that have the strongest support from living systems are demographic. In Lamont Cole's classic 1954 paper, he came to the conclusion that: "For an annual species, the absolute gain in intrinsic population growth which could be achieved by changing to the perennial reproductive habit would be exactly equivalent to adding one individual to the average litter size," (Lamont, 1954).

For example, imagine two species—an iteroparous species that has annual litters averaging three offspring each, and a semelparous species that has one litter of four, and then dies. These two species have the same rate of population growth, which suggests that even a tiny fecundity advantage of one additional offspring would favor the evolution of semelparity. This is known as Cole's paradox. In his analysis, Cole assumed that there was no mortality of individuals of the iteroparous species, even seedlings. Twenty years later, Charnov and Schaffer (1973) showed that reasonable differences in adult and juvenile mortality yield much more reasonable costs of semelparity, essentially solving Cole's paradox. An even more general demographic model was produced by Young (1981). These demographic models have been more successful than the other models when tested with real-world systems. It has been shown that semelparous species have higher expected adult mortality, making it more economical to put all reproductive effort into the first (and therefore final) reproductive episode (Young, 1990; Lesica & Young, 2005).

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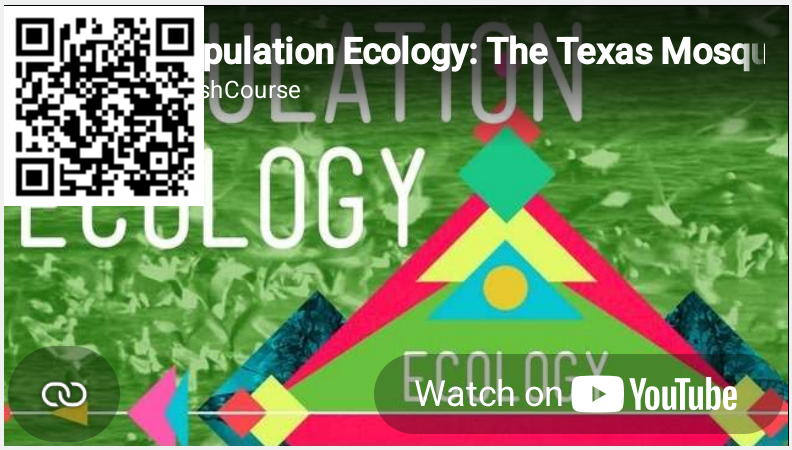
CHAPTER OVERVIEW

Chapter 9: The Ecology of Populations

Learning Objectives

- Describe how ecologists measure population size and density
- Summarize the types of population distribution
- Identify how the carrying capacity of habitats may change
- Describe how natural selection and environmental adaptation led to the evolution of particular life history patterns
- Explain the characteristics of and differences between exponential and logistic growth patterns
- Identify how population growth is regulated
- Predict the ecological consequences of unregulated growth
- Analyze the factors leading to exponential human population growth and its impacts

Video



This 11-minute video summarizes much of the content of Unit 4.2

9.1: What is Population Ecology?
9.2: Life Histories and Natural Selection
9.3: Population Demography
9.3.1: Scientist Spotlight - Jessie Isabelle Price
9.3: Population Dynamics and Regulation
9.4: Population Models
9.5: Human Population Growth

Summary

Populations are one of the major levels of biological organization, and "population thinking" plays a key role since Darwin in ecology and evolutionary biology. Currently, many researchers and natural resource managers are trained as population ecologists, from academics who study basic questions in evolutionary ecology to government scientists who determine catch limits for fisheries. In this chapter we define what populations are, their key features considered by basic and applied ecologists, and the techniques used out in the field to study populations. We'll also introduce key the key ecological concepts such of population regulation, density independence and density dependence which will be elaborated on in the next chapter.

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9.1: What is Population Ecology?

What is Population Ecology?

- Please read and watch the following Mandatory Resources
- Reading the material for understanding, and taking notes during videos, will take approximately ___ minutes.
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Population Ecology

Thousands of bird species breed and reproduce in North America. Some, like the American Robin (*Turdus migratorius*), are widespread, and can be found building nests and raising their young throughout North America. Others, like Kirtland's Warbler (*Setophaga kirtlandii)* breed almost entirely within a single state (Fig. 9.1.1); a few, like the Cozumel thrasher (*Toxostoma guttatum*) and Socorro mockingbird (*Mimus graysoni*) are found only on single small islands. Population ecologists study what determines the occurrence and abundance of species in space and time: their geographic ranges, population sizes and densities, and what factors result in them being so rare or common.

Population ecology is the branch of ecology that works to understand the patterns and processes of change over time or space for populations of a single species. A **species** is typically defined as a group of organisms capable of interbreeding. For some species, all of the members of the species occur in the same geographic area and could potentially meet and interbreed during their lifetimes. Most species, however, can be divided into geographically separate populations. Individuals within a single population are likely to interact and perhaps inter-breed, while those from different populations will only come into contact if there is long-range movement between the populations, known as **dispersal**.

? Exercise 9.1.1

The study of population ecology focuses on the _____.

a. number of individuals of one species in an area and how and why that number changes over time
b. processes driving interactions within and among different species within an area
c. adaptations that enable individuals to live in specific habitats
d. Plants and animals living in an enclosed area

Answer

a. number of individuals of one species in an area and how and why that number changes over time

Populations

Populations can be described by their size, density, or spatial extent. One species that currently consists of a single population is the Kirtland's warbler (*Setophaga kirtlandii*), a North American songbird. Almost all members of this species occur in the northern part of the state of Michigan in the United States, eastern Wisconsin, and southern Ontario (Fig. 9.1.1). In contrast, the Spotted Owl (*Strix occidentalis*) is a species with many distinct populations throughout the western United States, southern Canada, and central Mexico.



Figure 9.1.1: Left: A male Kirtland's Warbler in Michigan, USA. Right: Core habitat area of Kirtland's Warbler. Sources: Left - Photo by J. Trick, US Fish and Wildlife Service and accessed via Wikipedia https://bit.ly/KIWA_01. Used under the Creative Commons License CC BY 2.0. Right - Google Earth: https://bit.ly/3ofgDK1

For both species and populations, patterns of distribution and abundance can be measured in several ways. These include:

1. Size: How many total individuals there are?
2. Density: How many individuals per unit of area?
3. Dispersion: How are individuals in a population arranged spatially relative to another? Do they occur in clumps or are they evenly spread apart?
4. Occupancy: Does a species or member of a population occur in a given habitat, or is it absent?
5. Population distribution: Where does a population occur in space?
6. Geographic range: What are the furthest geographic limits of where a species occurs?

In addition to static characteristics of size and distribution, populations are dynamic and fluctuate based on a number of factors: seasonal and yearly changes in the environment, natural disasters such as forest fires and volcanic eruptions, and competition for resources between and within species. To study these many facets of a population's biology, ecologists use both systematic field observations to determine its current status, and mathematical tools to characterize how it responds to changes in the biotic and abiotic environments.

Population size

Population size is the actual number of organisms in a population. This is often of great interest to biologists – especially those working in forestry, wildlife management and conservation – and most of our basic population models work with population sizes. A **complete census** is one way to determine population size and entails counting each individual present within the population. This occurs in some well-studied populations, such as the Kasekela population of chimpanzees in Gombe National Park, Tanzania (Pusey et al. 2008), and the Seychelles Warbler on islands in the Indian Ocean off the coast of East Africa (Burt et al. 2016).

Although it is the most accurate methodology, counting every individual in a population can be difficult, if not impossible. In most cases, ecologists can only attempt to estimate the population size, "**N**", by using well-designed field studies and statistics. Indeed, some population ecologists specialize in developing mathematical and statistical models to accurately estimate population size, such as mark-recapture models and camera-trapping methods (detailed in Unit 4.2.4). Often, however, we do not have good estimates of the size of a population itself, but factors that should be correlated with the population size, such as the number of animals harvested by hunters or trapped by ecologists or the density of dung found during a survey.

Data that we think correlates with actual abundance constitutes a **population index**. Index data are cheaper to collect than the data needed for formal estimates of population size such as the mark-recapture methods discussed below, but can be biased and provide an inaccurate sense of the status of a population (Stephens et al. 2015). Ideally, an index should be validated by checking its correlation with rigorous estimates of population size. For example, the abundance of large mammals such as lions, elephants and tigers is frequently indexed by the frequency of their tracks or scat. To determine the reliability of an indirect measure of population size, Belant et al. (2019) compared an index based on lion tracks to a formal estimate of population size. Unfortunately, the commonly used index of lion abundance based on their tracks overestimated abundance.

When species become **endangered** researchers often try to determine - or at least estimate - the number of individuals surviving. For example, with only approximately 4000 individuals, Kirtland's Warbler is the rarest species breeding in the continental United States and was considered critically endangered throughout most of the 20th century. Researchers therefore worked each spring to determine as best as possible how many male warblers had established territories and were trying to attract mates.

Species that are economically important or are central players in ecosystem functioning are also often monitored intensively. Since the middle of the 20th century the abundance of Wildebeest (*Connochaetes taurinus*) in the Serengeti ecosystem of East Africa has been intensively monitored by aircraft (Fig. 9.1.2). The population was considered to be small in the 1960s when it numbered around 250,000, but by the 1990s had grown to over 1 million (Mduma et al. 1999).

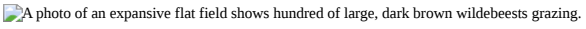


Figure 9.1.2 Wildebeest in Maasi Mara. Source: Photo by Bjørn Christian Tørrissen, http://bjornfree.com/galleries.html.

Population density

While population size is a total count of individuals, **population density** is how many individuals occur in a given area of space. It is therefore a measure of **relative abundance**. For animals and trees, this is often the estimated number of animals per hectare (a hectare is 100 m by 100 m, or 2.47 acres). For plants, insects, and other smaller organisms this is often the number per square meter.

Kirtland's Warbler is a **habitat specialist** (species that can thrive in a specialized subset of environmental conditions) and only nests in forests dominated by a single conifer, the Jack Pine (*Pinus banksiana*). Moreover, it only nests in Jack Pines of a certain age (5-20 years) and density (>3000 pines per hectare; Donner et al. 2018). When conditions are optimal, there is usually one breeding pair of warblers per 70 hectares, or 1.4 pairs per 100 hectares (Densities are usually reported for standard areas such as 1 square meter, 100 hectares, etc.).

Estimates of population density are often much easier to obtain than estimates of total population size. Population density can be converted to a rough estimate population size through simple multiplication. If there are 1.4 pairs per hectare of good habitat, and

there are 2800 hectares of habitat, we can calculate the number of pairs as 1.4*2000 = 2800 pairs. Two things are key to this calculation, however: first, the estimate of density is accurate, and second, the estimate of the amount of good habitat is accurate.

Occupancy

Occupancy is simply whether a given species or member of a population occurs in a habitat patch, fragment, or area. Often it can be very difficult to count the number of individuals or determine their density; instead of asking a question like "*How many owls are there in this forest?*" it's relatively easier to ask "*Are there* any *owls present in this forest?*" It can be very time-consuming to do counts or determine density, which can limit researchers' ability to study multiple sites or locations. Focusing on determining just the presence or absence of a population in a habitat often allows researchers to study a larger area.

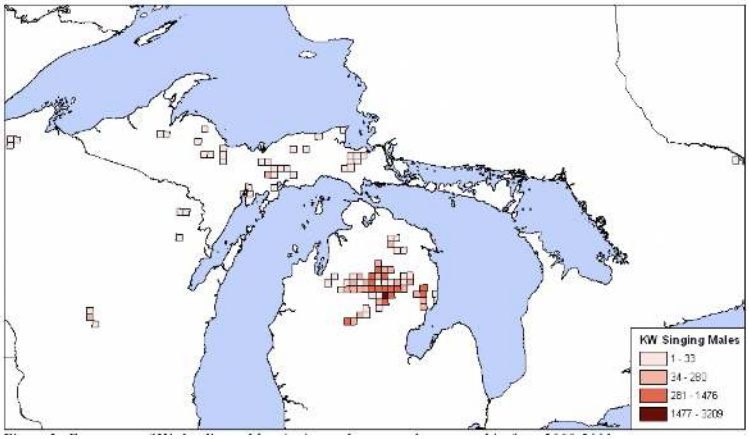


Figure 9.1.4: Frequency of Kirtland's warbler singing males counted per township from 2000-2011. Source: U.S. Fish and Wildlife Service.

Kirtland's Warbler is currently increasing its **population size** and is being found in stands of Jack Pine outside of the state of Michigan (Figure 9.1.4). Since the warbler's population is increasing, researchers are more interested in doing occupancy surveys to determine which patches of forest warblers are occurring in rather than determining exactly how many warblers are in these forests (Richards 2008).

Camera traps and occupancy studies can be used to determine if a species has become locally extinct. Giodano, Tumenta and Iongh (2017) carried out a camera-trap based occupancy study of Waza National Park in Cameroon. While they confirmed the occupancy of lions in the park, no leopards (*Panthera pardus*) were photographed. Since lions and leopards are typically similarly difficult to detect and lions were detected, they concluded that there were no longer any leopards occupying the park.

Distribution

In addition to measuring simple density, further information about a population can be obtained by looking at the distribution of the individuals. Species **distribution patterns** summarize the spatial relationship between members of a population within a habitat at a particular point in time. In other words, they show whether members of the population live close together or far apart, and what patterns are evident when they are spaced apart.

Individuals in a population can be more or less equally spaced apart, distributed randomly with no predictable pattern, or clustered in groups. These are known as uniform, random, and clumped distribution patterns, respectively (Fig. 9.1.5). **Uniform distribution** can occur in plants and is thought to result from competition for below-ground resources such as water, or secretion of substances inhibiting the growth of nearby individuals, a phenomenon called **allelopathy**. In animals like penguins that nest in large colonies, uniform dispersion can occur due to territorial behavior. An example of **random distribution** occurs with dandelion and other plants that have wind-dispersed seeds that germinate wherever they happen to fall in a favorable environment. A **clumped distribution** may be seen in plants that drop their seeds straight to the ground, such as oak trees, or animals that live in groups (schools of fish or herds of elephants). Clumped distribution may also be a function of habitat heterogeneity. Thus, the distribution pattern of the individuals within a population provides more information about how they interact with each other than does a simple density measurement. Just as lower density species might have more difficulty finding a mate, solitary species with a random distribution might have a similar difficulty when compared to social species clumped together in groups.

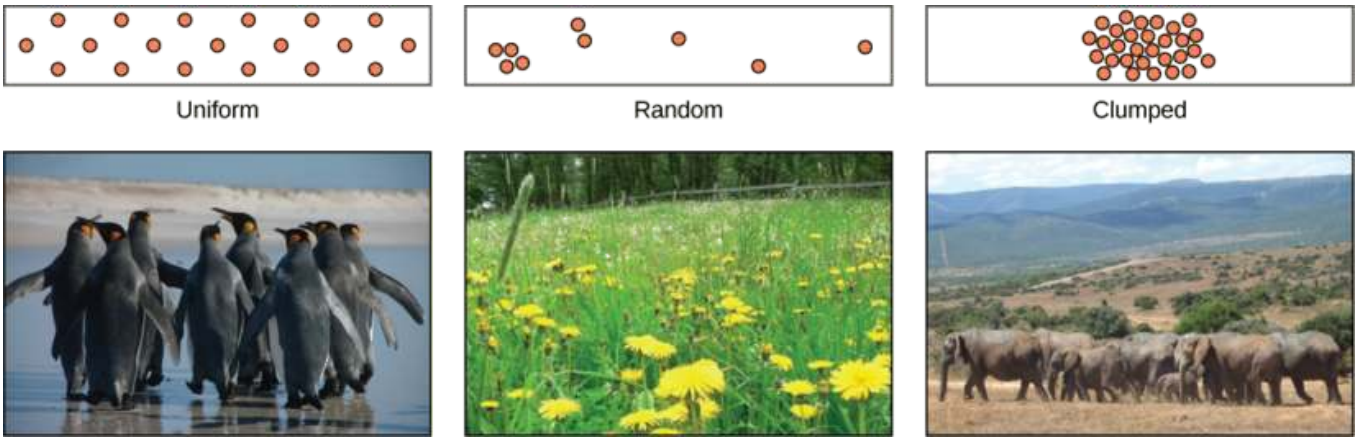


Figure 9.1.5: Species may have uniform, random, or clumped distribution. Territorial birds such as penguins tend to have uniform distribution. Plants such as dandelions with wind-dispersed seeds tend to be randomly distributed. Animals such as elephants that travel in groups exhibit clumped distribution. (credit a: modification of work by Ben Tubby; credit b: modification of work by Rosendahl; credit c: modification of work by Rebecca Wood)

Video



In this 3-minute video, see examples of the various types of distribution patterns populations exhibit across space (note that "aggregated" in the film is the same as clumped in the text above).
Question after watching: Which presented example is surprising to you and why?

Niches

Populations distributions are limited to suitable habitats. In ecology, a **niche** is the match of a species to a specific environmental condition. It describes how an organism or population responds to the distribution of environmental resources (abiotic components of the environment) and predators, pathogens, and competitors (biotic components of the environment). The geographic range of a species can be viewed as a spatial reflection of its niche, along with characteristics of the geographic template and the species that influence its potential to colonize. The **fundamental geographic range** of a species is the area it occupies in which environmental conditions are favorable, without restriction from barriers to disperse or colonize (Lomolino et al 2009). A species will be confined to its **realized geographic range** when confronting biotic interactions or abiotic barriers that limit dispersal, a more narrow subset of its larger fundamental geographic range.

An early study on ecological niches conducted by Joseph H. Connell analyzed the environmental factors that limit the range of a barnacle (*Chthamalus stellatus*) on Scotland's Isle of Cumbrae (Connell 1961). In his experiments, Connell described the dominant features of *C. stellatus* niches and provided explanation for their distribution on intertidal zone of the rocky coast of the Isle. Connell described the upper portion of C. stellatus's range as limited by the barnacle's ability to resist dehydration during periods of low tide. The lower portion of the range was limited by interspecific interactions, namely competition with a cohabiting barnacle species and predation by a snail (Connell 1961). By removing the competing *B. balanoides*, Connell showed that *C. stellatus* was able to extend the lower edge of its realized niche in the absence of competition. These experiments demonstrate how biotic and abiotic factors limit the distribution of an organism.

Range and Habitat

Population distribution is the geographic area where a particular population of a species occurs. This area of occupancy is determined by the local availability of appropriate habitat. A species' **geographic range** is the total geographic area occupied by a species. A term that can sometimes be confused with geographic range is home range. Geographic range refers to the entire spatial area a species can be found in, while a **home range** refers to an area utilized and perhaps defended by a single organism.

A species' current geographic range is often very different from its historical range. Factors such as habitat loss, hunting, and climate change can all reduce the distribution of populations and the species' overall geographic range. For example, lions previously ranged broadly over Africa, Western Asia, the Middle East and India (Fig. 9.1.6).

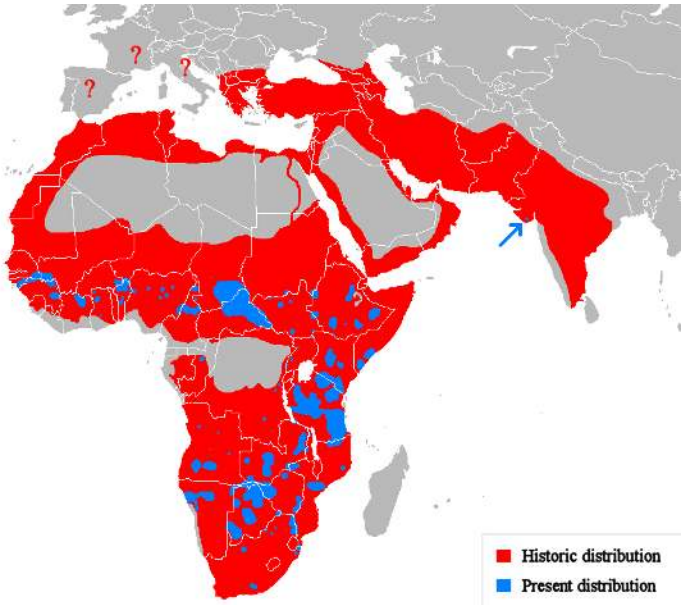


Figure 9.1.6: Historical (red) and present (blue) distribution of lions (*Panthera leo*). Source: Tommyknocker (Wikipedia), based on a map created by 'The African Lion Environmental Research Trust (ALERT).

Bald Eagles can be found breeding in almost every state of the USA and most provinces of Canada. Its geographic range therefore encompasses almost all of North America north of Mexico. In contrast, Golden Eagles breed almost exclusively in western Canada, the western United States, and Mexico. The Golden Eagle's range therefore is restricted to the western part of the continent and Mexico.

Some species are **habitat generalists** (species that can thrive in a wide variety of environmental conditions) and their populations spread out almost continuously across a landscape. American Robins, for example, can breed in parks, urbanized areas, farms, and the edges of forest. Other species are **habitat specialists** and only occur in specific places where a certain type of ecosystem occurs. Aquatic species also often occur in isolated populations because their habitat is necessarily bounded by the extent of the lake, wetland, or waterway they occur in.

The Northern Spotted Owl is a **subspecies** of spotted owl that is a habitat specialist that only occurs in old-growth forests in the Pacific Northwest of North America (British Columbia, Washington, Oregon, California). While much of the Pacific Northwest is still forested, most forests are less than 100 years old and don't have the large, old trees that the owls nest in. The extent of each population of owls is therefore limited by the size of each patch of old growth forest.

As noted above, Kirtland's warblers are habitat specialists, which means that the species only reside in the Jack Pine Forests of northern Michigan and a few adjacent states and Canadian provinces. Subsequently, this phenomenon is referred to by biologists as a restricted range. A restricted range species refers to a species in which the range is so small, there is basically a single population. This results in the population distribution and geographic range is essentially the same.

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9.2: Life Histories and Natural Selection

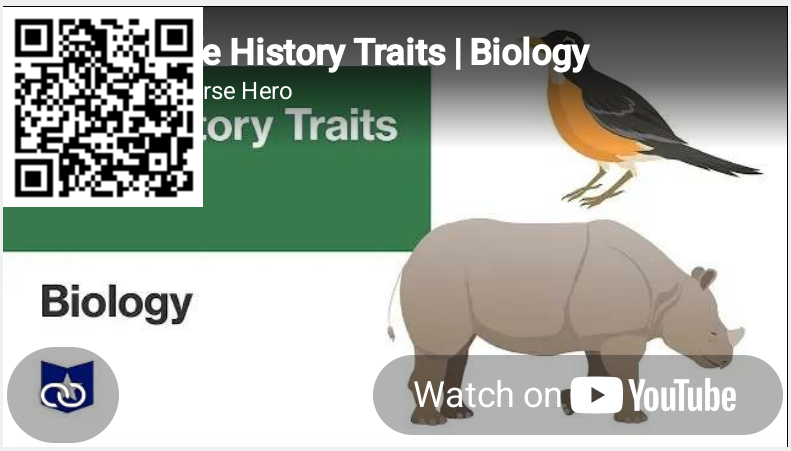
Life Histories and Natural Selection

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Learning Objectives

- Describe how life history patterns are influenced by natural selection
- Explain different life history patterns and how different reproductive strategies affect species' survival
- Describe how natural selection and environmental adaptation leads to the evolution of particular life-history patterns

Video



In this 4-minute video, learn how life history traits include significant life events of a species, such as reproductive rate and reproductive lifespan.
Question after watching: How do these traits relate to natural selection?

Life History Theory

Life history theory is an analytical framework designed to study the diversity of life history strategies used by different organisms throughout the world, as well as the causes and results of the variation in their life cycles. It is a theory of biological evolution that seeks to explain aspects of organisms' anatomy and behavior by reference to the way that their life histories—including their reproductive development and behaviors, post-reproductive behaviors, and lifespan (length of time alive)—have been shaped by natural selection. A life history strategy is the "age- and stage-specific patterns" and timing of events that make up an organism's life, such as birth, weaning, maturation, death, etc. These events, notably juvenile development, age of sexual maturity, first reproduction, number of offspring and level of parental investment, senescence and death, depend on the physical and ecological environment of the organism.

The theory was developed in the 1950s and is used to answer questions about topics such as organism size, age of maturation, number of offspring, life span, and many others. In order to study these topics, life history strategies must be identified, and then models are constructed to study their effects. Finally, predictions about the importance and role of the strategies are made, and these predictions are used to understand how evolution affects the ordering and length of life history events in an organism's life, particularly the lifespan and period of reproduction. Life history theory draws on an evolutionary foundation, and studies the effects of natural selection on organisms, both throughout their lifetime and across generations. It also uses measures of evolutionary

fitness to determine if organisms are able to maximize or optimize this fitness, by allocating resources to a range of different demands throughout the organism's life. It serves as a method to investigate further the "many layers of complexity of organisms and their worlds".

Organisms have evolved a great variety of life histories, from Pacific salmon, which produce thousands of eggs at one time and then die, to human beings, who produce a few offspring over the course of decades. The theory depends on principles of evolutionary biology and ecology and is widely used in other areas of science.



Figure 9.2.1: A swallowtail butterfly hatches from a chrysalis. Image: Pixabay

Life cycle

All organisms follow a specific sequence in their development, beginning with gestation and ending with death, which is known as the life cycle. Events in between usually include birth, childhood, maturation, reproduction, and senescence, and together these comprise the life history strategy of that organism. The major events in this life cycle are usually shaped by the demographic qualities of the organism. Some are more obvious shifts than others, and may be marked by physical changes—for example, teeth erupting in young children. Some events may have little variation between individuals in a species, such as length of gestation, but other events may show a lot of variation between individuals, such as age at first reproduction. Life cycles can be divided into two major stages: growth and reproduction. These two cannot take place at the same time, so once reproduction has begun, growth usually ends. This shift is important because it can also affect other aspects of an organism's life, such as the organization of its group or its social interactions.

Each species has its own pattern and timing for these events, often known as its ontogeny, and the variety produced by this is what life history theory addresses. Evolution then works upon these stages to ensure that an organism adapts to its environment. For example, a human, between being born and reaching adulthood, will pass through an assortment of life stages, which include: birth, infancy, weaning, childhood and growth, adolescence, sexual maturation, and reproduction. All of these are defined in a specific biological way, which is not necessarily the same as the way that they are commonly used. In life history theory, evolution works on the life stages of particular species (e.g., length of juvenile period) but is also discussed for a single organism's functional, lifetime adaptation. In both cases, researchers assume adaptation—processes that establish fitness.

Traits

There are at least seven traits that are traditionally recognized as important in life history theory. The trait that is seen as the most important for any given organism is the one where a change in that trait creates the most significant difference in that organism's level of fitness. In this sense, an organism's fitness is determined by its changing life history traits. The way in which evolutionary forces act on these life history traits serves to limit the genetic variability and heritability of the life history strategies, although there are still large varieties that exist in the world.

Commonly studied life history traits:

1. size at birth
2. growth pattern
3. age and size at maturity
4. number, size, and sex ratio of offspring
5. age- and size-specific reproductive investments

6. age- and size-specific mortality schedules
7. length of life.

Life History Patterns and Energy Budgets

Energy is required by all living organisms for their growth, maintenance, and reproduction; at the same time, energy is often a major limiting factor in determining an organism's survival. Plants, for example, acquire energy from the sun via photosynthesis, but must expend this energy to grow, maintain health, and produce energy-rich seeds to produce the next generation. Animals have the additional burden of using some of their energy reserves to acquire food. Furthermore, some animals must expend energy caring for their offspring. Thus, all species have an energy budget: they must balance energy intake with their use of energy for metabolism, reproduction, parental care, and energy storage (such as bears building up body fat for winter hibernation).

Parental Care and Fecundity

Fecundity is the potential reproductive capacity of an individual within a population. In other words, fecundity describes how many offspring could ideally be produced if an individual has as many offspring as possible, repeating the reproductive cycle as soon as possible after the birth of the offspring. In animals, fecundity is inversely related to the amount of parental care given to an individual offspring. Species, such as many marine invertebrates, that produce many offspring usually provide little if any care for the offspring (they would not have the energy or the ability to do so anyway). Most of their energy budget is used to produce many tiny offspring. Animals with this strategy are often self-sufficient at a very early age. This is because of the energy tradeoff these organisms have made to maximize their evolutionary fitness. Because their energy is used for producing offspring instead of parental care, it makes sense that these offspring have some ability to be able to move within their environment and find food and perhaps shelter. Even with these abilities, their small size makes them extremely vulnerable to predation, so the production of many offspring allows enough of them to survive to maintain the species.

Animal species that have few offspring during a reproductive event usually give extensive parental care, devoting much of their energy budget to these activities, sometimes at the expense of their own health. This is the case with many mammals, such as humans, kangaroos, and pandas. The offspring of these species are relatively helpless at birth and need to develop before they achieve self-sufficiency.

Plants with low fecundity produce few energy-rich seeds (such as coconuts and chestnuts) with each having a good chance to germinate into a new organism; plants with high fecundity usually have many small, energy-poor seeds (like orchids) that have a relatively poor chance of surviving. Although it may seem that coconuts and chestnuts have a better chance of surviving, the energy tradeoff of the orchid is also very effective. It is a matter of where the energy is used, for large numbers of seeds or for fewer seeds with more energy.

Early versus Late Reproduction

The timing of reproduction in a life history also affects species survival. Organisms that reproduce at an early age have a greater chance of producing offspring, but this is usually at the expense of their growth and the maintenance of their health. Conversely, organisms that start reproducing later in life often have greater fecundity or are better able to provide parental care, but they risk that they will not survive to reproductive age. Examples of this can be seen in fishes. Small fish like guppies use their energy to reproduce rapidly, but never attain the size that would give them defense against some predators. Larger fish, like the bluegill or shark, use their energy to attain a large size, but do so with the risk that they will die before they can reproduce or at least reproduce to their maximum. These different energy strategies and tradeoffs are key to understanding the evolution of each species as it maximizes its fitness and fills its niche. In terms of energy budgeting, some species "blow it all" and use up most of their energy reserves to reproduce early before they die. Other species delay having reproduction to become stronger, more experienced individuals and to make sure that they are strong enough to provide parental care if necessary.

Single versus Multiple Reproductive Events

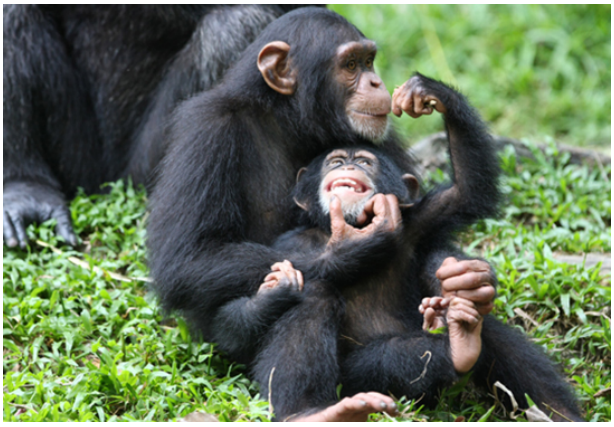
Some life history traits, such as fecundity, timing of reproduction, and parental care, can be grouped together into general strategies that are used by multiple species. **Semelparity** occurs when a species reproduces only once during its lifetime and then dies. Such species use most of their resource budget during a single reproductive event, sacrificing their health to the point that they do not survive. Examples of semelparity are bamboo, which flowers once and then dies, and the Chinook salmon (Figure 9.2.3a), which

uses most of its energy reserves to migrate from the ocean to its freshwater nesting area, where it reproduces and then dies. Scientists have posited alternate explanations for the evolutionary advantage of the Chinook's post-reproduction death: a programmed suicide caused by a massive release of corticosteroid hormones, presumably so the parents can become food for the offspring, or simple exhaustion caused by the energy demands of reproduction; these are still being debated.

Iteroparity describes species that reproduce repeatedly during their lives. Some animals are able to mate only once per year, but survive multiple mating seasons. The pronghorn antelope is an example of an animal that goes into a seasonal estrus cycle ("heat"): a hormonally induced physiological condition preparing the body for successful mating (Figure 9.2.3b). Females of these species mate only during the estrus phase of the cycle. A different pattern is observed in primates, including humans and chimpanzees, which may attempt reproduction at any time during their reproductive years, even though their menstrual cycles make pregnancy likely only a few days per month during ovulation (Figure 9.2.3c).



a b



c

Figure 9.2.2: The (a) Chinook salmon mates once and dies. The (b) pronghorn antelope mates during specific times of the year during its reproductive life. Primates, such as humans and (c) chimpanzees, may mate on any day, independent of ovulation. (credit a: modification of work by Roger Tabor, USFWS; credit b: modification of work by Mark Gocke, USDA; credit c: modification of work by "Shiny Things"/Flickr)

? Optional Activity 9.2.1

Which of the following is associated with long-term parental care?

a. few offspring
b. many offspring
c. semelparity
d. fecundity

Answer

a. few offspring

Trade-offs

An essential component of studying life history strategies is identifying the trade-offs[1] that take place for any given organism. Energy use in life history strategies is regulated by thermodynamics and the conservation of energy, and the "inherent scarcity of resources", so not all traits or tasks can be invested in at the same time. Thus, organisms must choose between tasks, such as growth, reproduction, and survival, prioritizing some and not others. For example, there is a trade-off between maximizing body size and maximizing lifespan, and between maximizing offspring size and maximizing offspring number. This is also sometimes seen as a choice between quantity and quality of offspring. These choices are the trade-offs that life history theory studies.

One significant trade-off is between **somatic effort** (towards growth and maintenance of the body) and **reproductive effort** (towards producing offspring). Since an organism cannnot put energy towards doing these simultaneously, many organisms have a period where energy is put just toward growth, followed by a period where energy is focused on reproduction, creating a separation of the two in the life cycle. Thus, the end of the period of growth marks the beginning of the period of reproduction. Another fundamental trade-off associated with reproduction is between mating effort and parenting effort. If an organism is focused on raising its offspring, it cannot devote that energy to pursuing a mate.

An important trade-off in the dedication of resources to breeding has to do with predation risk: organisms that have to deal with an increased risk of predation often invest less in breeding. This is because it is not worth as much to invest a lot in breeding when the benefit of such investment is uncertain.

These trade-offs, once identified, can then be put into models that estimate their effects on different life history strategies and answer questions about the selection pressures that exist on different life events. Over time, there has been a shift in how these models are constructed. Instead of focusing on one trait and looking at how it changed, scientists are looking at these trade-offs as part of a larger system, with complex inputs and outcomes.

The idea of **constraints** is closely linked to the idea of trade-offs discussed above. Because organisms have a finite amount of energy, the process of trade-offs acts as a natural limit on the organism's adaptations and potential for fitness. These limits can be physical, developmental, or historical, and they are imposed by the existing traits of the organism.

Populations can adapt and thereby achieve an "optimal" life history strategy that allows the highest level of fitness possible (fitness maximization). There are several methods from which to approach the study of optimality, including energetic and demographic. Achieving optimal fitness also encompasses multiple generations, because the optimal use of energy includes both the parents and the offspring. For example, "optimal investment in offspring is where the decrease in total number of offspring is equaled by the increase of the number who survive". Optimality is important for the study of life history theory because it serves as the basis for many of the models used, which work from the assumption that natural selection, as it works on a life history traits, is moving towards the most optimal group of traits and use of energy. This base assumption, that over the course of its life span an organism is aiming for optimal energy use, then allows scientists to test other predictions. However, actually gaining this optimal life history strategy cannot be guaranteed for any organism.

An organism's allocation of resources ties into several other important concepts, such as trade-offs and optimal strategies. The best possible allocation of resources is what allows an organism to achieve an optimal life history strategy and obtain the maximum level of fitness, and making the best possible choices about how to allocate energy to various trade-offs contributes to this. The allocation of resources also plays a role in variation, because the different resource allocations by different species create the variety of life history strategies.

Unpredictable environments

Many factors can determine the evolution of an organism's life history, especially the unpredictability of the environment. A very unpredictable environment—one in which resources, hazards, and competitors may fluctuate rapidly—selects for organisms that produce more offspring earlier in their lives, because it is never certain whether they will survive to reproduce again. Mortality rate, the number of individuals who die per 1000 over a given time, may be the best indicator of a species' life history: organisms with high mortality rates—the usual result of an unpredictable environment—typically mature earlier than those species with low mortality rates, and give birth to more offspring at a time. A highly unpredictable environment can also lead to plasticity, in which individual organisms can shift along the spectrum of r-selected vs. K-selected life histories to suit the environment.

Early Theories about Life History: *K*-selected and *r*-selected Species

While reproductive strategies play a key role in life histories, they do not account for important factors like limited resources and competition. The regulation of population growth by these factors can be used to introduce a classical concept in population biology, that of *K*-selected versus *r*-selected species.

By the second half of the twentieth century, the concept of K- and r-selected species was used extensively and successfully to study populations. The concept relates not only reproductive strategies, but also to a species' habitat and behavior, especially in the way that they obtain resources and care for their young. It includes length of life and survivorship factors as well. For this analysis, population biologists have grouped species into the two large categories—*K*-selected and *r*-selected—although they are really two ends of a continuum (Table 9.2.1).

Table 9.2.1: Characteristics of *K*-selected and *r*-selected species

Characteristics of *K*-selected species	Characteristics of *r*-selected species
Mature late	Mature early
Greater longevity	Lower longevity
Increased parental care	Decreased parental care
Increased competition	Decreased competition
Fewer offspring	More offspring
Larger offspring	Smaller offspring

***K*-selected** species are species selected by stable, predictable environments. Populations of *K*-selected species tend to exist close to their carrying capacity (hence the term *K*-selected) where intraspecific competition is high. These species have few, large offspring, a long gestation period, and often give long-term care to their offspring. While larger in size when born, the offspring are relatively helpless and immature at birth. By the time they reach adulthood, they must develop skills to compete for natural resources. In plants, scientists think of parental care more broadly: how long fruit takes to develop or how long it remains on the plant are determining factors in the time to the next reproductive event. Examples of *K*-selected species are primates including humans), elephants, and plants such as oak trees (Figure 9.2.3a).

Oak trees grow very slowly and take, on average, 20 years to produce their first seeds, known as acorns. As many as 50,000 acorns can be produced by an individual tree, but the germination rate is low as many of these rot or are eaten by animals such as squirrels. In some years, oaks may produce an exceptionally large number of acorns, and these years may be on a two- or three-year cycle depending on the species of oak (*r*-selection).

As oak trees grow to a large size and for many years before they begin to produce acorns, they devote a large percentage of their energy budget to growth and maintenance. The tree's height and size allow it to dominate other plants in the competition for sunlight, the oak's primary energy resource. Furthermore, when it does reproduce, the oak produces large, energy-rich seeds that use their energy reserve to become quickly established (*K*-selection).



(a) K-selected species



(b) r-selected species

Figure 9.2.3: (a) Elephants are considered K-selected species as they live long, mature late, and provide long-term parental care to few offspring. Oak trees produce many offspring that do not receive parental care, but are considered K-selected species based on longevity and late maturation. (b) Dandelions and jellyfish are both considered r-selected species as they mature early, have short lifespans, and produce many offspring that receive no parental care.

In contrast, ***r*-selected** species have a large number of small offspring (hence their *r* designation (Table 9.2.1). This strategy is often employed in unpredictable or changing environments. Animals that are *r*-selected do not give long-term parental care and the offspring are relatively mature and self-sufficient at birth. Examples of *r*-selected species are marine invertebrates, such as jellyfish, and plants, such as the dandelion (Figure 9.2.3b). Dandelions have small seeds that are wind dispersed long distances. Many seeds are produced simultaneously to ensure that at least some of them reach a hospitable environment. Seeds that land in inhospitable environments have little chance for survival since their seeds are low in energy content. Note that survival is not necessarily a function of energy stored in the seed itself.

? Optional Activity 9.2.2

The following statements compare r-selected and K-selected species. Identify the statement that makes an accurate comparison.

a. r-selected and K-selected species both have limitations in the amount of energy they can invest in reproduction, so they both use similar strategies.
b. r-selected and K-selected species both have limitations in the amount of energy they can invest in reproduction, but they use completely different strategies.
c. r-selected and K-selected species use similar reproductive strategies but r-selected species require less energy to reproduce than K-selected species.
d. r-selected and K-selected species use different reproductive strategies because r-selected species require less energy to reproduce than K-selected species.

Answer

b. r-selected and K-selected species both have limitations in the amount of energy they can invest in reproduction, but they use completely different strategies.

Modern Theories of Life History

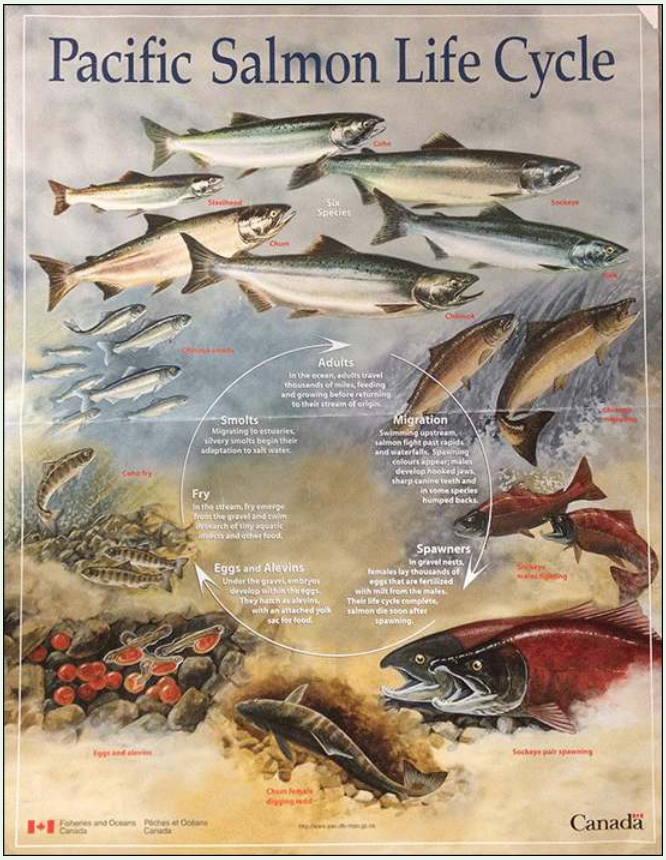
The *r*- and *K*-selection theory, although accepted for decades and used for much groundbreaking research, has now been reconsidered, and many population biologists have abandoned or modified it. Over the years, several studies attempted to confirm the theory, but these attempts have largely failed. Many species were identified that did not follow the theory's predictions. Furthermore, the theory ignored the age-specific mortality of the populations which scientists now know is very important. New demographic-based models of life history evolution have been developed which incorporate many ecological concepts included in *r*- and *K*-selection theory and population age structure and mortality factors. These are discussed in the next sections.

Indigenous Connections: The Life Histories of Salmon

Salmon is an essential resource to many First Nations people and communities in BC. Salmon is found in almost every part of BC, with the exception of northeast regions that are in the Peace and McKenzie River watersheds. For thousands of years, First Nations peoples have developed an intricate understanding and knowledge about salmon, including the interconnectedness of salmon with other life forms. Before contact, salmon was a foundational trade item, contributing significantly to the economy and social structure of First Nations societies. Salmon helped to ensure the sustenance of large, vibrant populations of people. First Nations developed a myriad of technologies to capture and preserve the salmon. The value and respect that the people had for the salmon is reflected in the representation of salmon in traditional stories, songs, dances, and art throughout BC.

The Pacific salmon life cycle depends on the species. Some spend hardly any time in natal streams; some spend years. Some mature at two years of age; some mature at five. Some live for only a couple of years; others live for ten. And some, like Steelhead and Cutthroat, can spawn more than once. Despite these variations, we can still make some general observations about the life stages of salmon.

All Pacific salmon are anadromous, which means they start in freshwater (streams, lakes, rivers, etc.), migrate to the ocean, then return home to spawn and die.



Adult spawners often journey for hundreds of miles to return to the waters their parents spawned in, and where they themselves were born. If they make it back, evading all sorts of obstacles—predation, competition, environmental impediments, the males and females court, and ultimately breed. At the crucial moment, the male releases sperm and the female releases eggs… at precisely the same time.

The eggs and sperm float in a fog of milt to the bottom of the stream or lake bed where the female has painstakingly prepared a redd (aka nest), which, covered with gravel, is expected to protect the eggs until they are ready to hatch.

While new salmon are preparing to enter the world, their parents die (usually only days after spawning), making them semelparous. Their bodies remain in the water or along the shore to decay and/or be eaten by other species. In this way, they continue to nourish the environment around them.

Adapted from:

- First Nations Education Steering Committee (2019). *FNESC/FNSA Secondary Science First Peoples Teacher Resource Guide. Unit 6: Salmon and Interconnectedness.* 298 pp. http://www.fnesc.ca/wp/wp-content/uploads/2019/08/PUBLICATION-SCIENCE-FIRST-PEOPLES-Secondary-TRG-2019.pdf
- Pacific Salmon Foundation 2022 (https://psf.ca/)



A 7-minute short about the importance and life cycle of wild Pacific salmon.



A 15-minute video entitled "St'at'imc: The Salmon People"

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9.3: Population Demography

Population Demography

- Please read and watch the following Mandatory Resources
- Reading the material for understanding, and taking notes during videos, will take approximately ___ minutes.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Describe how ecologists measure population size and density
- Describe three different patterns of population distribution
- Use life tables to estimate mortality rates
- Describe the three types of survivorship curves and relate them to specific populations

Populations are dynamic entities. Populations consist all of the species living within a specific area, and populations fluctuate based on a number of factors: seasonal and yearly changes in the environment, natural disasters such as forest fires and volcanic eruptions, and competition for resources between and within species. The statistical study of population dynamics, **demography**, uses a series of mathematical tools to investigate how populations respond to changes in their biotic and abiotic environments. Many of these tools were originally designed to study human populations. For example, **life tables**, which detail the life expectancy of individuals within a population, were initially developed by life insurance companies to set insurance rates. In fact, while the term “demographics” is commonly used when discussing humans, all living populations can be studied using this approach.

Population Size and Density

The study of any population usually begins by determining how many individuals of a particular species exist, and how closely associated they are with each other. Within a particular habitat, a population can be characterized by its population size (*N*), the total number of individuals, and its **population density**, the number of individuals within a specific area or volume. Population size and density are the two main characteristics used to describe and understand populations. For example, populations with more individuals may be more stable than smaller populations based on their genetic variability, and thus their potential to adapt to the environment. Alternatively, a member of a population with low population density (more spread out in the habitat), might have more difficulty finding a mate to reproduce compared to a population of higher density. As is shown in Figure 9.3.1, smaller organisms tend to be more densely distributed than larger organisms.

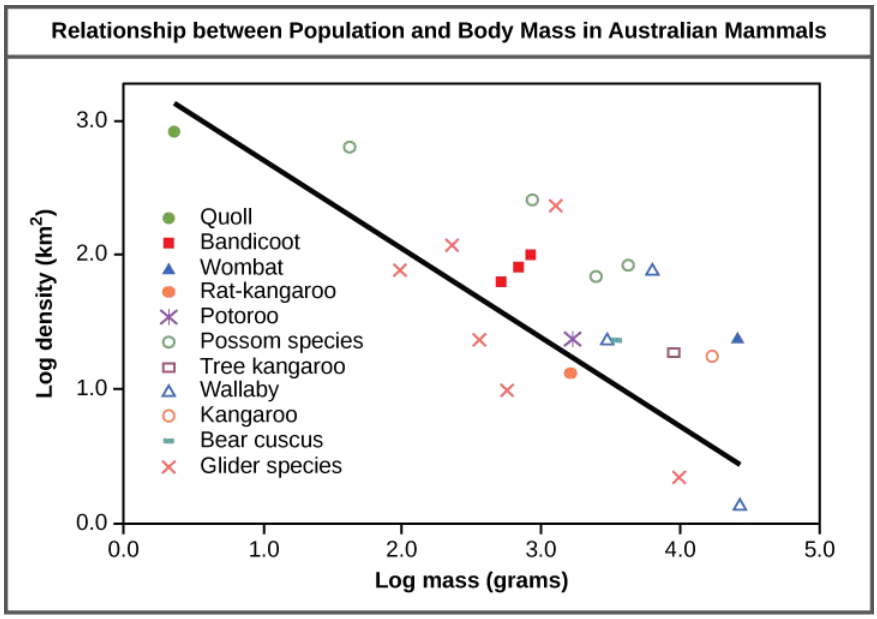


Figure 9.3.1: Australian mammals show a typical inverse relationship between population density and body size.

? Optional Activity 9.3.1

Figure 9.3.1: As this graph shows, population density typically decreases with increasing body size. Why do you think this is the case?

Answer

Smaller animals require less food and other resources, so the environment can support more of them.

Population Research Methods

The most accurate way to determine population size is to simply count all of the individuals within the habitat. However, this method is often not logistically or economically feasible, especially when studying large habitats. Thus, scientists usually study populations by sampling a representative portion of each habitat and using this data to make inferences about the habitat as a whole. A variety of methods can be used to sample populations to determine their size and density.

Video



Ecologists are interested in the distribution of organisms within habitats, and use transects, quadrants, and other sampling methods to collect quantitative data, as you will see in this 5-minute video.
Question after watching: What type of technique would be used for mobile organisms?

Quadrat Sampling

For immobile organisms such as plants, or for very small and slow-moving organisms, a quadrat may be used. A **quadrat** is a way of marking off square areas within a habitat, either by staking out an area with sticks and string, or by the use of a wood, plastic, or metal square placed on the ground (Figure 9.3.2). After setting the quadrats, researchers then count the number of individuals that lie within their boundaries. Multiple quadrat samples are performed throughout the habitat at several random locations. All of this data can then be used to estimate the population size and population density within the entire habitat. The number and size of quadrat samples depends on the type of organisms under study and other factors, including the density of the organism. For example, if sampling daffodils, a 1 m^2 quadrat might be used whereas with giant redwoods, which are larger and live much further apart from each other, a larger quadrat of 100 m^2 might be employed. This ensures that enough individuals of the species are counted to get an accurate sample that correlates with the habitat, including areas not sampled.

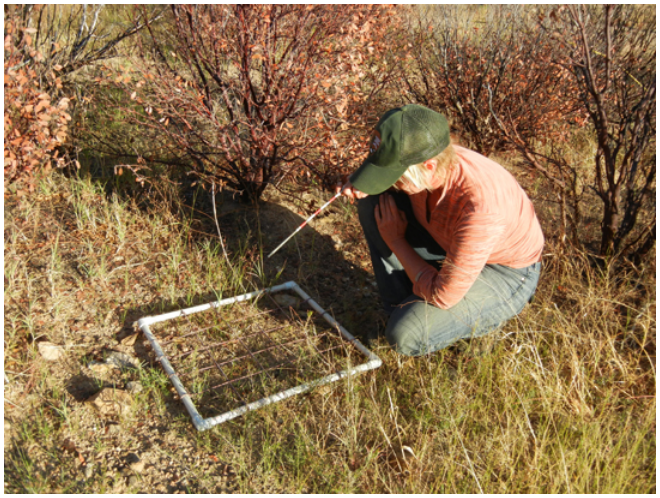


Figure 9.3.2: A scientist uses a quadrat to measure population size and density. (credit: NPS Sonoran Desert Network)

Distance Sampling Methods

Other techniques for sampling populations to estimate density or abundance are distance sampling methods (Figure 9.3.3). The main methods are based on **line transects** or **point transects**. Distance-based methods are frequently used for animals with observers making their observations while walking, riding in trucks, or in low-flying aircraft. They can also be used for tasks such as surveying for very rare trees or plants.

In this method of sampling, the data collected are the distances of the objects being surveyed from these randomly placed lines or points, and the objective is to estimate the average density of the objects within a region. When using line transects, the observer randomly places a straight line or follows some pre-planned route through the habitat of the population of interest, then walks the line or route. Whenever the researcher observes an object of interest (e.g., an animal of the type being surveyed), they record the observation, the distance from their current position to the object (r), as well as the angle of the detection to the transect line (θ). The distance of the object to the transect can then be calculated using trigonometry as $x = r * \sin(\theta)$. These distances x are the detection distances that will be analyzed in further modeling aspects of the population (e.g., population distribution in space).

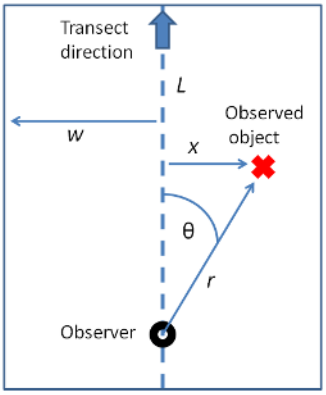
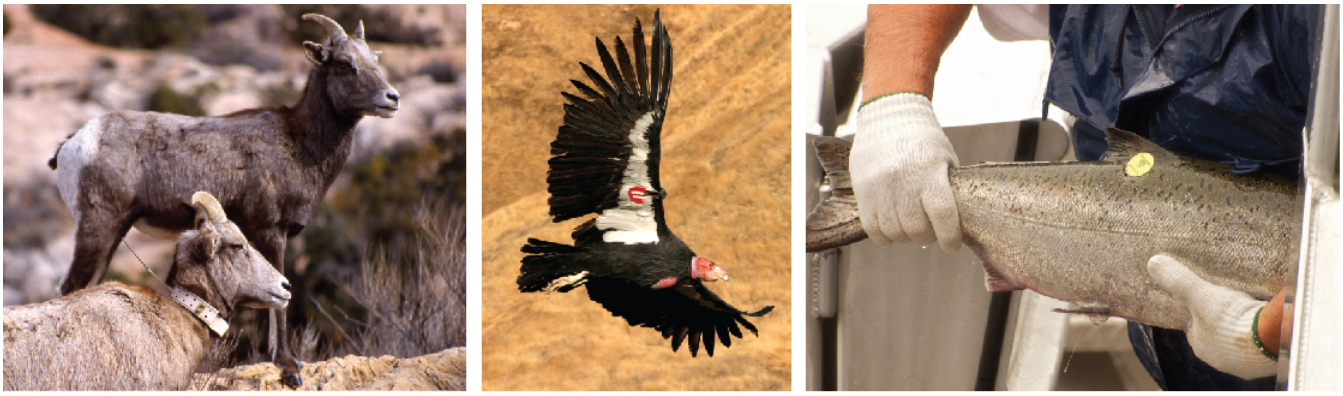


Figure 9.3.3: Basic distance sampling survey approach using line transects. A field observer detects an object and records distance *r* and angle *θ* to the transect line. This allows the calculation of object distance to the transect (*x*). All *x* from the survey are used to model how detectability decreases with distance from the transect, which allows estimation of total population density in the surveyed area. (Elmidae; CC-BY-4.0)

Mark and Recapture

For mobile organisms, such as mammals, birds, or fish, a technique called **mark and recapture** is often used. This method involves marking a sample of captured animals in some way (such as tags, bands, paint, or other body markings), and then releasing them back into the environment to allow them to mix with the rest of the population; later, a new sample is collected, including some individuals that are marked (recaptures) and some individuals that are unmarked (Figure 9.3.4).



(a) (b) (c)

Figure 9.3.4: Mark and recapture is used to measure the population size of mobile animals such as (a) bighorn sheep, (b) the California condor, and (c) salmon. (credit a: modification of work by Neal Herbert, NPS; credit b: modification of work by Pacific Southwest Region USFWS; credit c: modification of work by Ingrid Taylar)

Using the ratio of marked and unmarked individuals, scientists determine how many individuals are in the sample. From this, calculations are used to estimate the total population size. This method assumes that the larger the population, the lower the percentage of tagged organisms that will be recaptured since they will have mixed with more untagged individuals. For example, if 80 deer are captured, tagged, and released into the forest, and later 100 deer are captured and 20 of them are already marked, we can determine the population size (*N*) using the following equation:

$$\frac{\text{number marked first catch} * \text{total number of second catch}}{\text{number marked second catch}} = N$$

Using our example, the population size would be estimated at 400.

$$\frac{(80 * 100)}{20} = 400$$

Therefore, there are an estimated 400 total individuals in the original population.

There are some limitations to the mark and recapture method. Some animals from the first catch may learn to avoid capture in the second round, thus inflating population estimates. Alternatively, animals may preferentially be retrapped (especially if a food

reward is offered), resulting in an underestimate of population size. Also, some species may be harmed by the marking technique, reducing their survival. A variety of other techniques have been developed, including the electronic tracking of animals tagged with radio transmitters and the use of data from commercial fishing and trapping operations to estimate the size and health of populations and communities.

Camera Traps

Recently, great progress in estimating animal density has been made using camera traps (Fig. 9.3.5). These are especially useful for studying rare and nocturnal animals, such as predators. For example, lions (*Panthera leo*) are considered vulnerable to extinction and are most threatened in West Africa, where they are restricted to a few small national parks. In western-most West Africa lions occur only in Niokolo-Koba National Park in south-eastern Senegal. Mamadou Kane used camera traps to estimate the density of lions in Niokolo-Koba. While the entire park is 9130 km^2, Kane sampled an area of approximately 285.4 square kilometers within the highest quality lion habitat of the park. Kane estimated that there are about 3 lions per 100 square kilometers in this high-quality habitat (100 square kilometers is an area 10 km by 10 km). Three lions per 100 km^2 equals 0.03 per km^2. We can therefore estimate the total abundance in the study area as 0.03*285.4 = 8.6 lions.



Figure 9.3.5: A camera trap, for taking pictures of game on trails. This model is for hunting. Motion detector on top, lens in the middle, flash on the bottom, with a little LCD for showing how many pictures taken/left on the left. By Hustvedt CC BY-SA 3.0

? Optional Activity 9.3.2

Which of the following methods will tell an ecologist about both the size and density of a population?

a. mark and recapture
b. line transect
c. quadrat
d. camera trap

Answer

c. quadrat sampling

Demography

While population size and density describe a population at one particular point in time, scientists must use demography to study the dynamics of a population. **Demography** is the statistical study of population changes over time: birth rates, death rates, and life expectancies. Each of these measures, especially birth rates, may be affected by the population characteristics described above. For example, a large population size results in a higher birth rate because more potentially reproductive individuals are present. In contrast, a large population size can also result in a higher death rate because of competition, disease, and the accumulation of waste. Similarly, a higher population density or a clumped dispersion pattern results in more potential reproductive encounters between individuals, which can increase birth rate. Lastly, a female-biased sex ratio (the ratio of males to females) or age structure

(the proportion of population members at specific age ranges) composed of many individuals of reproductive age can increase birth rates.

In addition, the demographic characteristics of a population can influence how the population grows or declines over time. If birth and death rates are equal, the population remains stable. However, the population size will increase if birth rates exceed death rates; the population will decrease if birth rates are less than death rates. **Life expectancy** is another important factor; the length of time individuals remain in the population impacts local resources, reproduction, and the overall health of the population. These demographic characteristics are often displayed in the form of a life table.

Life Tables

Life tables provide important information about the life history of an organism. **Life tables** divide the population into age groups and often sexes, and show how long a member of that group is likely to live. They are modeled after actuarial tables used by the insurance industry for estimating human life expectancy. Life tables may include the probability of individuals dying before their next birthday (i.e., their mortality rate), the percentage of surviving individuals dying at a particular age interval, and their life expectancy at each interval.

An example of a life table is shown in Table 9.3.1 from a study of Dall mountain sheep, a species native to northwestern North America. Notice that the population is divided into age intervals (column A). The mortality rate (per 1000), shown in column D, is based on the number of individuals dying during the age interval (column B) divided by the number of individuals surviving at the beginning of the interval (Column C), multiplied by 1000.

$$\text{mortality rate} = \frac{\text{number of individuals dying}}{\text{number of individuals surviving}} * 1000$$

For example, between ages three and four, 12 individuals die out of the 776 that were remaining from the original 1000 sheep. This number is then multiplied by 1000 to get the mortality rate per thousand.

$$\text{mortality rate} = \frac{12}{776} * 1000 \approx 15.5$$

As can be seen from the mortality rate data (column D), a high death rate occurred when the sheep were between 6 and 12 months old, and then increased even more from 8 to 12 years old, after which there were few survivors. The data indicate that if a sheep in this population were to survive to age one, it could be expected to live another 7.7 years on average, as shown by the life expectancy numbers in the last column.

Table 9.3.1: Life Table of Dall Mountain Sheep[1]

Age interval (years)	Number dying in age interval out of 1000 born	Number surviving at beginning of age interval out of 1000 born	Mortality rate per 1000 alive at beginning of age interval	Life expectancy or mean lifetime remaining to those attaining age interval
0-0.5	54	1000	54.0	7.06
0.5-1	145	946	153.3	--
1-2	12	801	15.0	7.7
2-3	13	789	16.5	6.8
3-4	12	776	15.5	5.9
4-5	30	764	39.3	5.0
5-6	46	734	62.7	4.2
6-7	48	688	69.8	3.4
7-8	69	640	107.8	2.6
8-9	132	571	231.2	1.9
9-10	187	439	426.0	1.3
10-11	156	252	619.0	0.9
11-12	90	96	937.5	0.6
12-13	3	6	500.0	1.2
13-14	3	3	1000	0.7

Survivorship Curves

Another tool used by population ecologists is a **survivorship curve**, which is a graph of the number of individuals surviving at each age interval plotted versus time (usually with data compiled from a life table). These curves allow us to compare the life histories of different populations (Figure 9.3.6). Humans and most primates exhibit a **Type I survivorship curve** because a high percentage of offspring survive their early and middle years—death occurs predominantly in older individuals. These types of species usually have small numbers of offspring at one time, and they give a high amount of parental care to them to ensure their survival. Birds are an example of an intermediate or **Type II survivorship curve** because birds die more or less equally at each age interval. These organisms also may have relatively few offspring and provide significant parental care. Trees, marine invertebrates, and most fishes exhibit a **Type III survivorship curve** because very few of these organisms survive their younger years; however, those that make it to an old age are more likely to survive for a relatively long period of time. Organisms in this category usually have a very large number of offspring, but once they are born, little parental care is provided. Thus these offspring are “on their own” and vulnerable to predation, but their sheer numbers assure the survival of enough individuals to perpetuate the species.

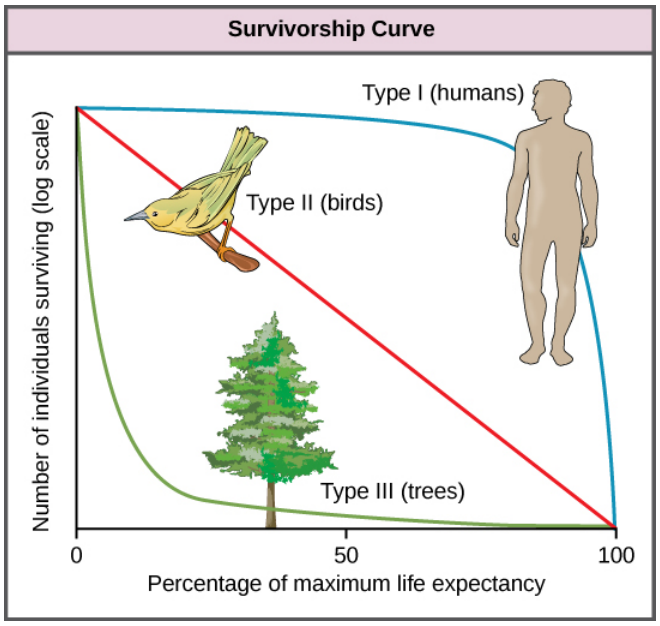


Figure 9.3.6: Survivorship curves show the distribution of individuals in a population according to age. Humans and most mammals have a Type I survivorship curve because death primarily occurs in the older years. Birds have a Type II survivorship curve, as death at any age is equally probable. Trees have a Type III survivorship curve because very few survive the younger years, but after a certain age, individuals are much more likely to survive.

? Optional Activity 9.3.3

Different species have different survival curves. A Type III survival curve would most likely be observed for _____.

a. whales
b. seals
c. salmon
d. polar bears

Answer

c. salmon

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9.3.1: Scientist Spotlight - Jessie Isabelle Price

In November 2021, Oxford University Press (OUP) made headlines when the company announced its 2021 Word of the Year - Vax. Given the coronavirus pandemic, words like “vax” and “vaccine” have dominated our language and everyday lives, so this comes as no surprise. In a report on the language of vaccines, OUP states that the origin of “vaccine” relates to the pioneering work of 18th century British physician Edward Jenner. *Vacca* is the Latin word for cow, and through his work with inoculation, “Jenner conceived the Latin expression *variolae vaccinae* as a name for cowpox” (OUP 2021). At first, the word “vaccine” only described inoculation against cowpox, but its usage was expanded to include multiple variations of the word in reference to immunization against other diseases. But surely, one Englishman could not be the end-all-be-all, sole champion of vaccination? Cue Jessie Isabelle Price.

Born in Montrose, Pennsylvania in 1930, Price was raised by a single mother and attended predominantly white public schools. After graduating from high school and being accepted into Cornell, she deferred for a year to prepare herself academically (Gillmer 2018). Price wanted to become a physician, but could not afford additional costs that the program required. Instead, she graduated with a Bachelors of Science in microbiology in 1953 and by 1959, Price had earned a Masters and PhD in bacteriology, pathology, and parasitology. Work from her dissertation, in which she studied *Pasteurella anatipestifer* infection in Pekin ducklings, was published in the journal *Avian Diseases*. Following her graduate studies, Price remained at Cornell as a research scientist focusing on “the identification and control of bacterial diseases in commercial white Pekin Ducklings.” (Gillmer 2018)

Although her career stretched beyond her time at the Cornell Duck Disease Research Laboratory, some of her most impactful work originated from her time there. For example, farmers internationally were losing ducklings due to respiratory disease, and Price discovered that they were dying of duck hepatitis, *Pasteurella multocida*, and *Escherichia coli* (Warren 1999). Not only did she uncover the source of this avian mortality, Price developed two vaccines that saved the poultry industry money, but more importantly prevented potential disease outbreaks in other bird species. Despite this monumental achievement, if asked about the history of vaccines, Jenner (or Fauci) is typically the only name that comes to mind.

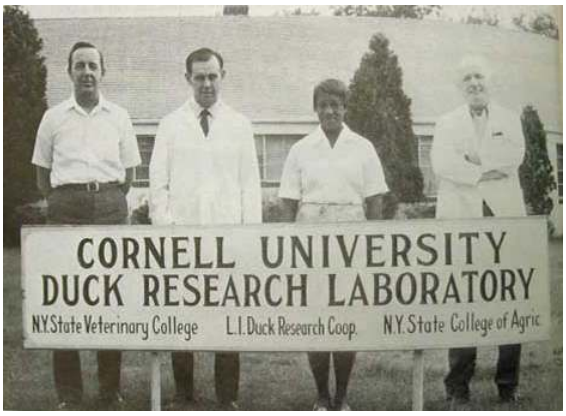


Figure 9.3.1.1**:** “Cornell University’s Duck Research Laboratory” provided by Cornell University is licensed under CC0 1.0.

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9.3: Population Dynamics and Regulation

How do populations change?

Changes in population size over time and the processes that cause these to occur are called **population dynamics**. How populations change in abundance over time is a major concern of **population ecology**, **wildlife ecology**, and **conservation biology**, and is related to questions asked in **evolutionary biology**. The **processes** and **mechanisms** that drive population change are varied and include **intraspecific competition** with members of the same population, **interspecific competition** between species, the availability of food or other resources, extreme weather, inbreeding, predators or parasites.

Populations are dynamic and frequently change size, density, or spatial extent

We can consider changes in populations from multiple angles. For example, Kirtland's Warbler (S*etophaga kirtlandii*) in North America is currently:

1. Increasing in the overall number of individuals (**population size**).
2. Increasing in the number of occupied habitat patches (**occupancy**).
3. Increasing in the geographic area it occurs in (**population distribution** and **species range**).

Importantly, since the warbler prefers a certain density of Jack Pine, its density within an occupied habitat also changes. Jack Pine stands are naturally prone to burning in **forest fires**, and are also logged for timber. As the density of trees changes due to these disturbances, the density of warblers changes. After a fire or logging there are few if any mature pine trees and therefore few warblers. Approximately five years after seedlings have sprouted and grown up to be the proper size, the density of warblers can increase. When pine forests get too old habitat conditions are not ideal for the warbler and their abundance declines.

Many studies of population growth focus on changes in population size

Though there are many dimensions to **spatial** and **temporal** population dynamics, discussions of population dynamics often center on changes in population size over time. Changes in population size are often displayed in a **time series graph** with time on the **x-axis** (usually in years) and population size (N) on the y-axis. General patterns of population dynamics in terms of population size include:

1. **Growth**: Growing larger than the current size (Snail kites: Figure 9.3.1.a)
2. **Decline**: Decreasing in abundance (Elk: Figure 9.3.1.b)
3. **Stability**: Staying approximately the same size over time (Wolves: Figure 9.3.1.c)
4. **Recovery**: Stability or growth following a period of decline. (Impala: Figure 9.3.1.d).
5. **Extirpation (local extinction):** Decline of one or more populations of a species to 0 (Kirtland's Warbler, Figure 9.3.2.a).
6. **Extinction**: Decline of all members of a species to 0 (Northern White Rhino, Figure 9.3.2.b).
7. **Cycles**: repeated patterns of growth followed by decline (Lynx: Figure 9.3.2.c)

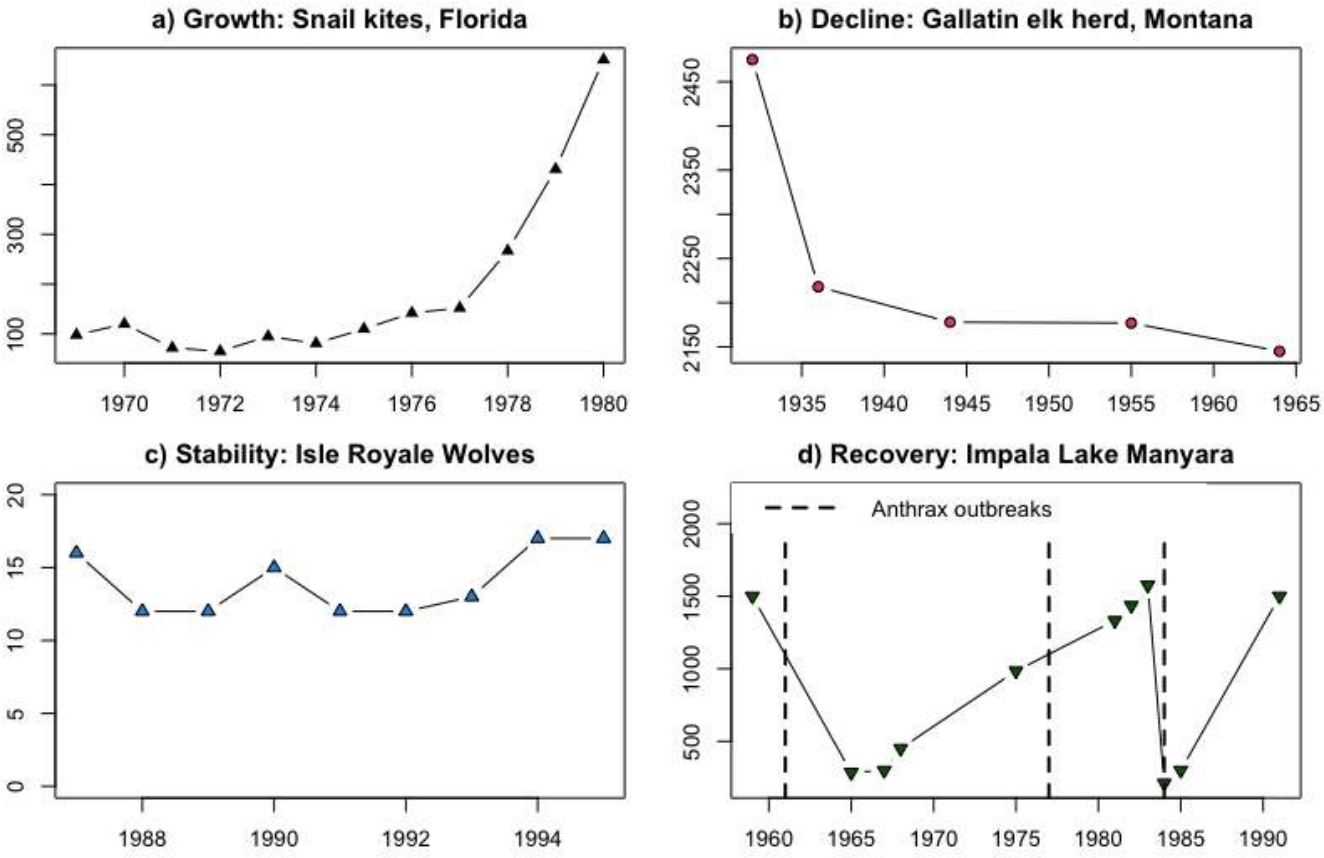


Figure 9.3.1**:** Common patterns of population change. The x-axis in all panels is the year and the y-axis is the number of individuals. a) Growth in a Florida Snail Kite (*Rostrhamus sociabilis*) population from 1970s to 1980s (Sykes 1983); b) Decline of the Gallatin, Montana herd of elk (*Cervus canadensis*) from the 1920s to 1960s (Peek et al. 1967); c) Stability of the Isle Royale, Michigan pack of wolves (*Canis lupus*) in the 1980s and 1990s (Peterson et al. 1998); d) Recovery after population crashes in the Lake Manyara National Park, Tanzania herd of impala (Prins and Weyerhaeuser 1987).

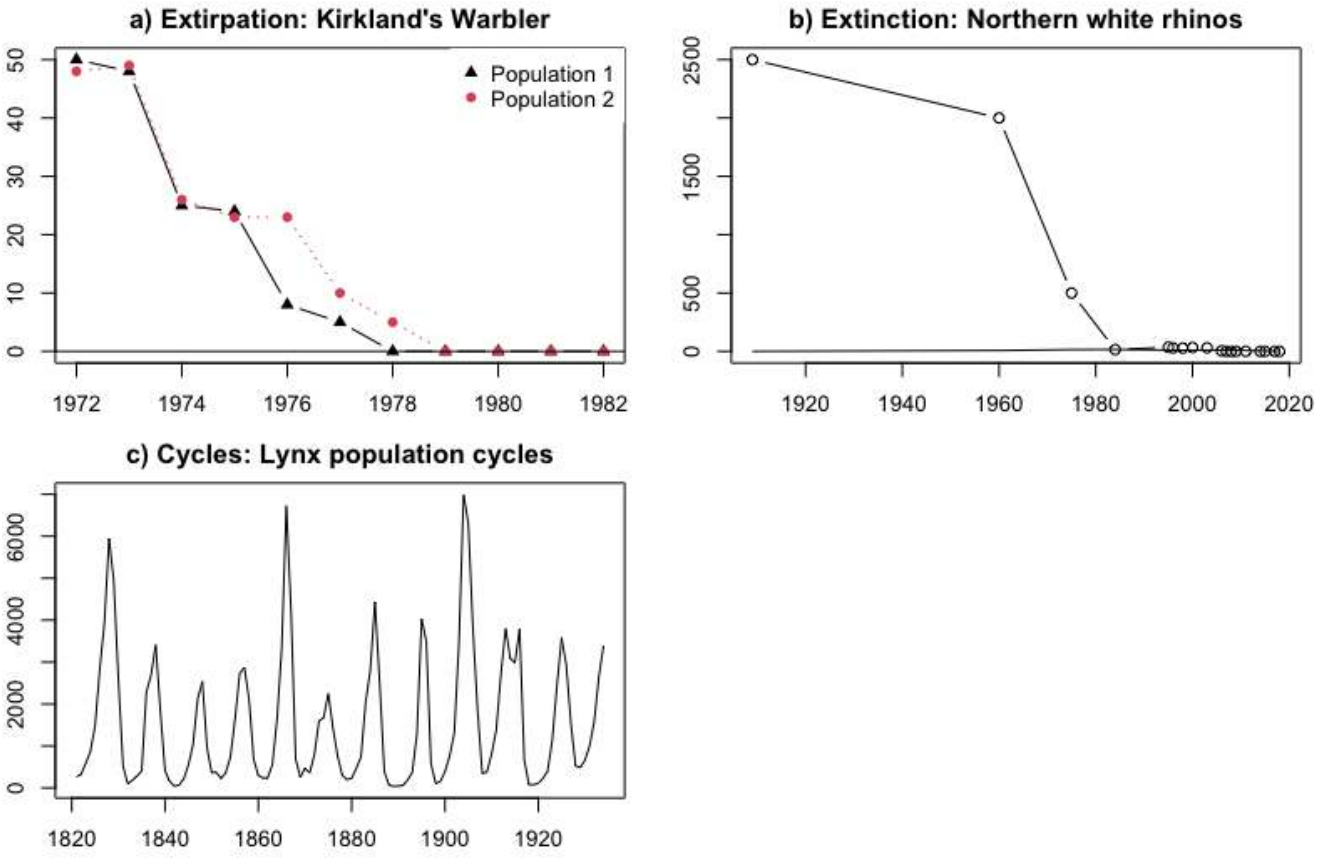


Figure 9.3.2**:** Common patterns of population change. The x-axis in all panels is the year. a) Decline to extirpation (local extinction) of Kirtland's Warbler in two populations (Probst 1986). The y-axis is the number of singing males; b) Decline to global extinction of the Northern White Rhinoceros (*Ceratotherium simum cottoni*), one of two subspecies of White Rhinos (Smith 2001, Emslie 2012). The y-axis is the total number of rhinos in the wild. c) Repeated cycling of the Canada lynx (*Lynx canadensis*; Campbell and Walker 1977). The y-axis is the number of lynx trapped, an index of population size.

Over the course of many years, a single population can display many of these dynamics. For example, Kirtland's Warbler populations were monitored by determining the number of males defending territories in their summer breeding habitat in the Great Lakes region North America, primarily Michigan. There were about 500 males with territories in the 1950s (Figure 9.3.3). The following changes occurred over the next 50 years after the species began being protected by the Endangered Species Act (Kepler et al. 1996):

1. **Decline** over the course of the 1960s to ~200 territories.
2. A period of **stability** at ~200 territories from 1975 to 1990.
3. Steady **growth** to >2500 from 1990 through 2020.

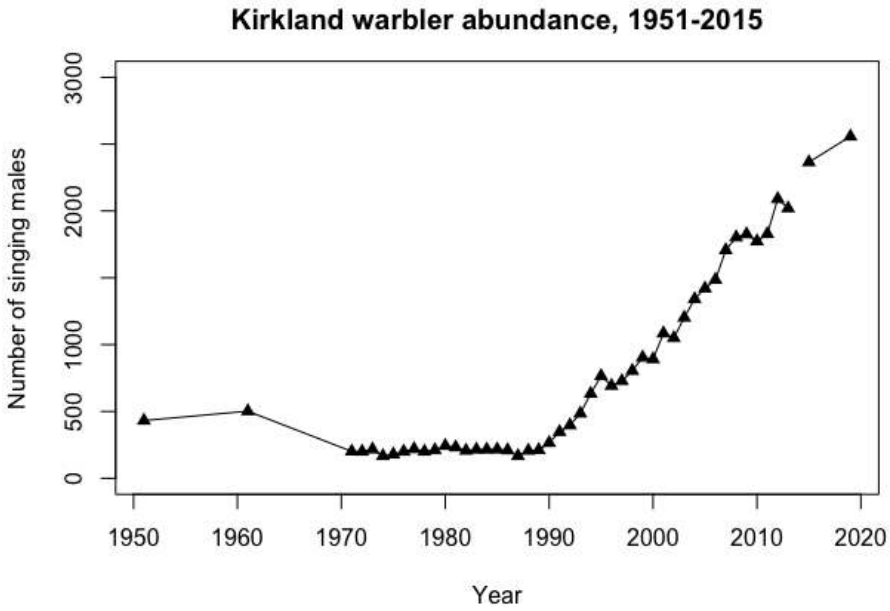


Figure 9.3.3**:** Number of singing Kirtland's Warbler (*Setophaga kirtlandii*) males, 1950 to 2020.

Models can be used to understand and predict population dynamics

Researchers who study population dynamics often use **mathematical models** to describe and predict population dynamics and understand what factors are driving those changes. For example, if there are 2500 Kirtland's Warblers in Michigan this year, can we predict how many will be around next year, or 10 years from now? Due to its small population size the Kirtland's Warbler was listed as an Endangered Species in 1967. In 2019 it was de-listed and now is considered "Near-threatened." Ecologists are very interested in using models to predict how large the Kirtland's Warbler population will be in the future, and what factors cause it to increase and decrease (Brown et al. 2019). In the next chapter we will explore the conceptual and mathematical tools ecologists use to understand population dynamics and predict their future trajectories.

Biotic interactions and abiotic conditions limit the sizes of populations

Population dynamics can be regulated in a variety of ways. These are grouped into **density-dependent** factors, in which the density of the population at a given time affects growth rate and mortality, and **density-independent** factors, which influence mortality in a population regardless of population density. Note that in the former, the effect of the factor on the population depends on the density of the population at onset. Conservation biologists want to understand both types because this helps them manage populations and prevent extinction or overpopulation.

Density-Dependent Regulation

Most density-dependent factors are biological in nature (biotic), and include predation, inter- and intraspecific competition, accumulation of waste, and diseases such as those caused by parasites. Usually, the denser a population is, the greater its mortality rate. For example, during intra- and interspecific competition, the reproductive rates of the individuals will usually be lower, reducing their population's rate of growth. In addition, low prey density increases the mortality of its predator because it has more difficulty locating its food source.

An example of density-dependent regulation is shown in Figure 9.3.4 with results from a study focusing on the giant intestinal roundworm (*Ascaris lumbricoides*), a parasite of humans and other mammals (Croll et al. 1982). Denser populations of the parasite exhibited lower fecundity: they contained fewer eggs. One possible explanation for this is that females would be smaller in more dense populations (due to limited resources) and that smaller females would have fewer eggs. This hypothesis was tested and disproved in a 2009 study which showed that female weight had no influence (Walker et al. 2009). The actual cause of the density-dependence of fecundity in this organism is still unclear and awaiting further investigation.

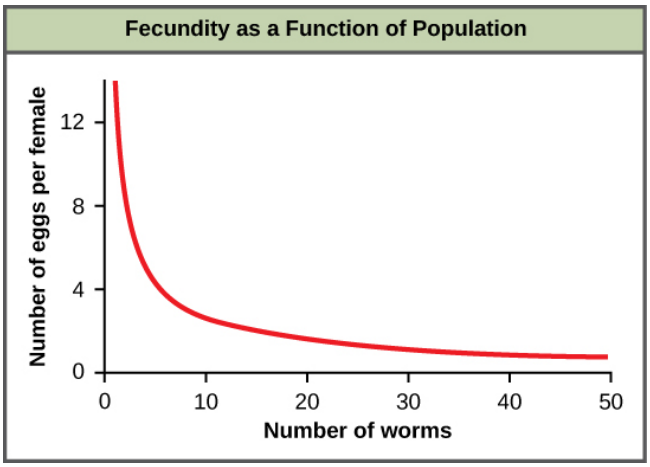


Figure 9.3.4**:** In this population of roundworms *Ascaris lumbricoides*, fecundity (number of eggs) decreases with population density (Croll et al. 1982).

Density-Independent Regulation and Interaction with Density-Dependent Factors

Many factors, typically physical or chemical in nature (abiotic), influence the mortality of a population regardless of its density, including weather, natural disasters, and pollution. An individual deer may be killed in a forest fire regardless of how many deer happen to be in that area. Its chances of survival are the same whether the population density is high or low. The same holds true for cold winter weather.

In real-life situations, population regulation is very complicated and density-dependent and independent factors can interact. A dense population that is reduced in a density-independent manner by some environmental factor(s) will be able to recover differently than a sparse population. For example, a population of deer affected by a harsh winter will recover faster if there are more deer remaining to reproduce.

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9.4: Population Models

Population Models

- Please read and watch the following Mandatory Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 1 hour.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Compare and contrast density-dependent growth regulation and density-independent growth regulation, giving examples
- Explain the characteristics of and differences between exponential and logistic growth patterns
- Give examples of exponential and logistic growth in wild animal populations

Although life histories describe the way many characteristics of a population (such as their age structure) change over time in a general way, population ecologists make use of a variety of methods to model population dynamics mathematically. These more precise models can then be used to accurately describe changes occurring in a population and better predict future changes. Certain models that have been accepted for decades are now being modified or even abandoned due to their lack of predictive ability, and scholars strive to create effective new models.

Population Dynamics

Changes in population size over time and the processes that cause these to occur are called **population dynamics**. How populations change in abundance over time is a major concern of population ecology, wildlife ecology, and conservation biology, and is related to questions asked in evolutionary biology. The processes and mechanisms that drive population change are varied and include intraspecific competition with members of the same population, interspecific competition between species, the availability of food or other resources, extreme weather, inbreeding, predators or parasites.

We can consider changes in populations from various measures of populations. For example, Kirtland's Warbler (S*etophaga kirtlandii*) in North America is currently:

1. Increasing in the overall number of individuals (population size).
2. Increasing in the number of occupied habitat patches (occupancy).
3. Increasing in the geographic area it occurs in (population distribution and species range).

Importantly, since the warbler prefers a certain density of Jack Pine, its density within an occupied habitat also changes. Jack Pine stands are naturally prone to burning in forest fires, and are also logged for timber. As the density of trees changes due to these disturbances, the density of warblers changes. After a fire or logging there are few if any mature pine trees and therefore few warblers. Approximately five years after seedlings have sprouted and grown up to be the proper size, the density of warblers can increase. When pine forests get too old habitat conditions are not ideal for the warbler and their abundance declines.

Population Size Over Time

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1. Growth: Growing larger than the current size (Snail kites: Figure 9.4.1a)
2. Decline: Decreasing in abundance (Elk: 9.4.1b)
3. Stability: Staying approximately the same size over time (Wolves: 9.4.1c)

4. Recovery: Stability or growth following a period of decline. (Impala: 9.4.1d)
5. Extirpation (local extinction): Decline of one or more populations of a species to 0 (Kirtland's Warbler, 9.4.2a).
6. Extinction: Decline of all members of a species to 0 (Northern White Rhino, 9.4.2b).
7. Cycles: repeated patterns of growth followed by decline (Lynx: 9.4.2c)

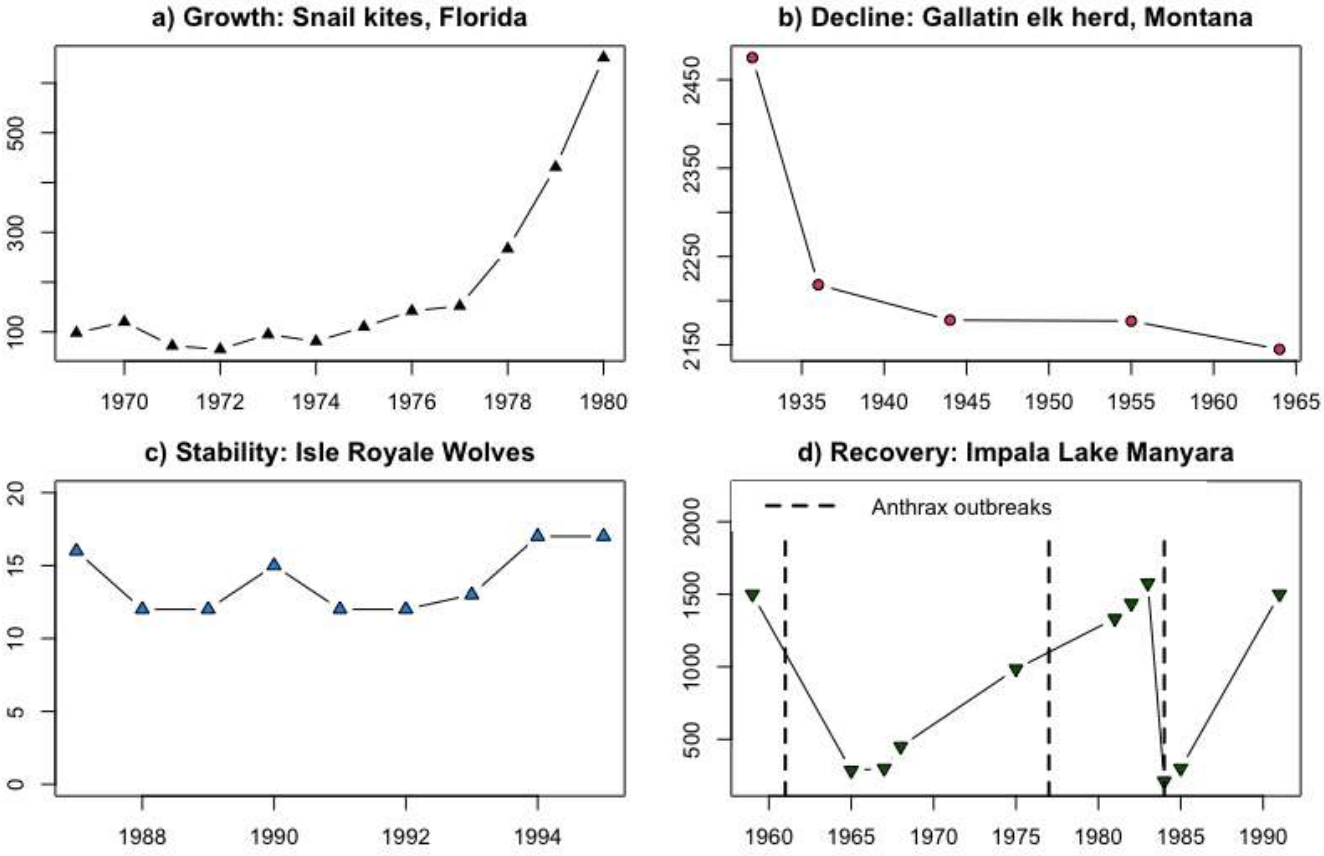


Figure 9.4.1: Common patterns of population change. The x-axis in all panels is the year and the y-axis is the number of individuals. a) Growth in a Florida Snail Kite (*Rostrhamus sociabilis*) population from 1970s to 1980s; b) Decline of the Gallatin, Montana herd of elk (*Cervus canadensis*) from the 1920s to 1960s; c) Stability of the Isle Royale, Michigan pack of wolves (*Canis lupus*) in the 1980s and 1990s; d) Recovery after population crashes in the Lake Manyara National Park, Tanzania herd of impala.

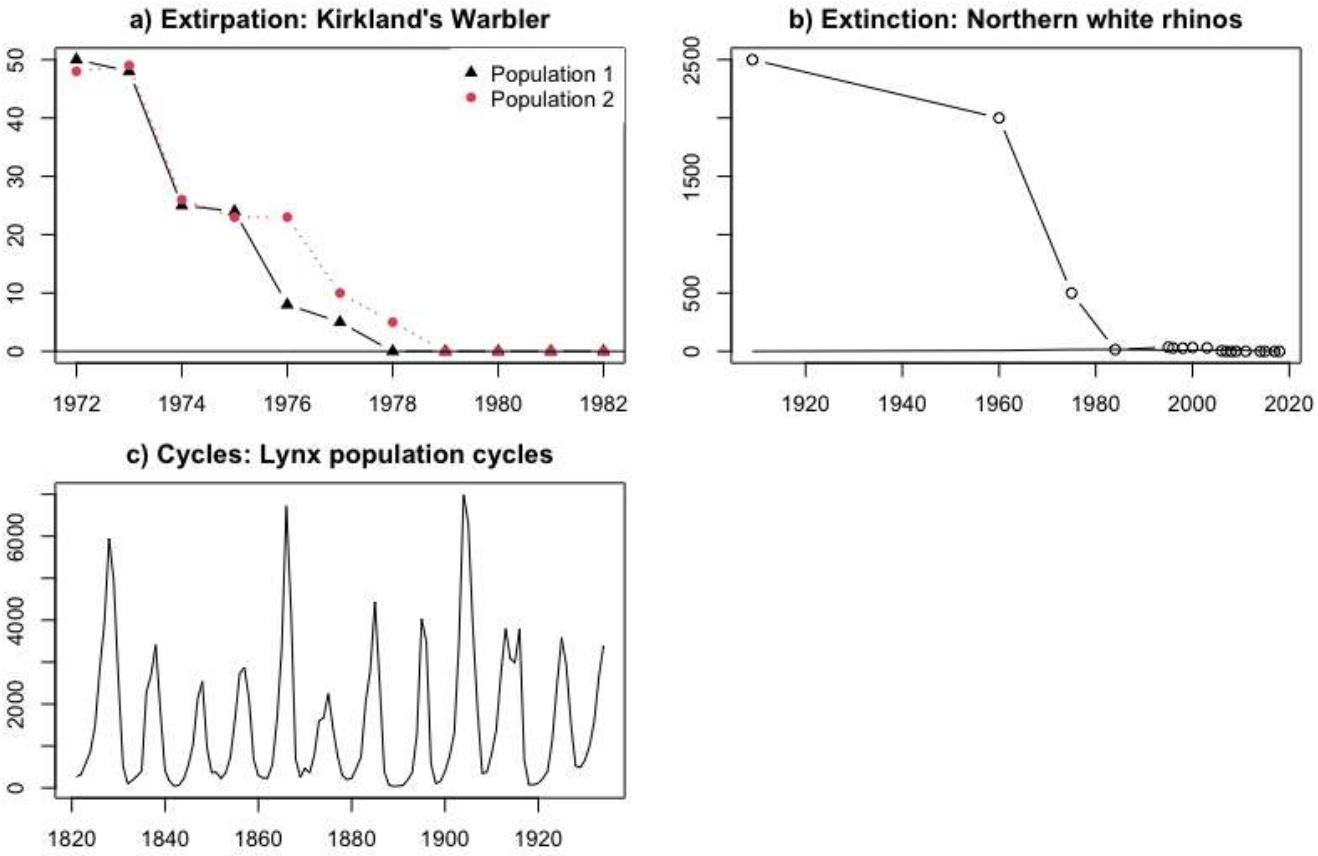


Figure 9.4.2: Common patterns of population change. The x-axis in all panels is the year. a) Decline to extirpation (local extinction) of Kirtland's Warbler in two populations. The y-axis is the number of singing males; b) Decline to global extinction of the Northern White Rhinoceros (*Ceratotherium simum cottoni*), one of two subspecies of White Rhinos. The y-axis is the total number of rhinos in the wild. c) Repeated cycling of the Canada lynx (*Lynx canadensis)*. The y-axis is the number of lynx trapped, an index of population size.

Mixed Dynamics

Over the course of many years, a single population can display many of these dynamics. For example, Kirtland's Warbler populations were monitored by determining the number of males defending territories in their summer breeding habitat in the Great Lakes region North America, primarily Michigan. There were about 500 males with territories in the 1950s (9.4.3). The following changes occurred over the next 50 years after the species began being protected by the Endangered Species Act:

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3. Steady growth to >2500 from 1990 through 2020.

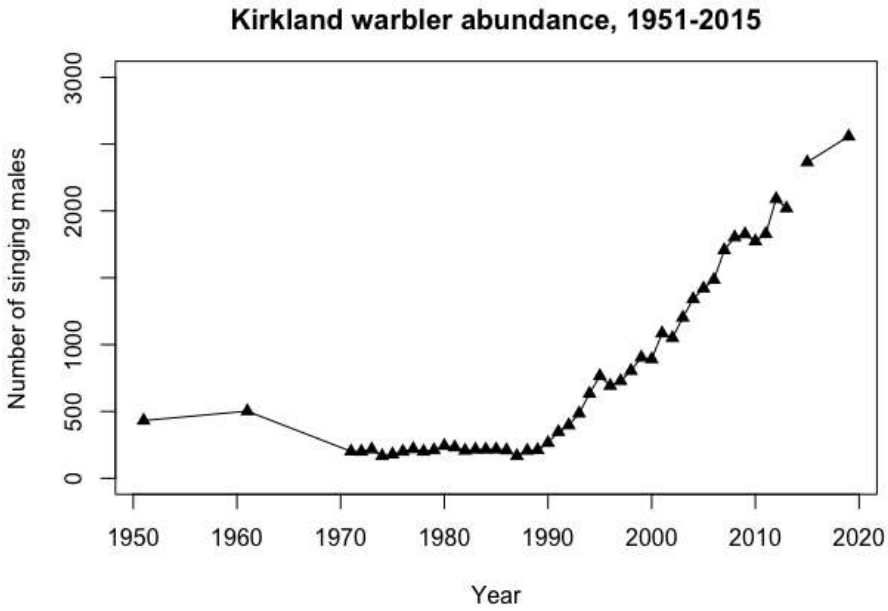


Figure 9.4.3: Number of singing Kirtland's Warbler (*Setophaga kirtlandii*) males, 1950 to 2020.

Population Modeling

Researchers who study population dynamics often use mathematical models to describe and predict population dynamics and understand what factors are driving those changes. For example, if there are 2500 Kirtland's Warblers in Michigan this year, can we predict how many will be around next year, or 10 years from now? Due to its small population size the Kirtland's Warbler was listed as an Endangered Species in 1967. In 2019 it was de-listed and now is considered "Near-threatened." Ecologists are very interested in using models to predict how large the Kirtland's Warbler population will be in the future, and what factors cause it to increase and decrease. Below, we explore the conceptual and mathematical tools ecologists use to understand population dynamics and predict their future trajectories.

Types of Growth: Exponential and Logistic

Exponential Growth

Charles Darwin, in his theory of natural selection, was greatly influenced by the English clergyman Thomas Malthus. Malthus published a book in 1798 stating that populations with unlimited natural resources grow very rapidly, and then population growth decreases as resources become depleted. This accelerating pattern of increasing population size is called exponential growth.

The best example of exponential growth is seen in bacteria. Bacteria are prokaryotes that reproduce by prokaryotic fission. This division takes about an hour for many bacterial species. If 1,000 bacteria are placed in a large flask with an unlimited supply of nutrients (so the nutrients will not become depleted), after an hour, there is one round of division and each organism divides, resulting in 2,000 organisms—an increase of 1,000. In another hour, each of the 2,000 organisms will double, producing 4,000, an increase of 2,000 organisms. After the third hour, there should be 8,000 bacteria in the flask, an increase of 4,000 organisms. The important concept of exponential growth is that the population growth rate—the number of organisms added in each reproductive generation—is accelerating; that is, it is increasing at a greater and greater rate. After 1 day and 24 of these cycles, the population would have increased from 1,000 to more than 16 billion. When the population size, *N*, is plotted over time, a J-shaped growth curve is produced (Figure 9.4.4).

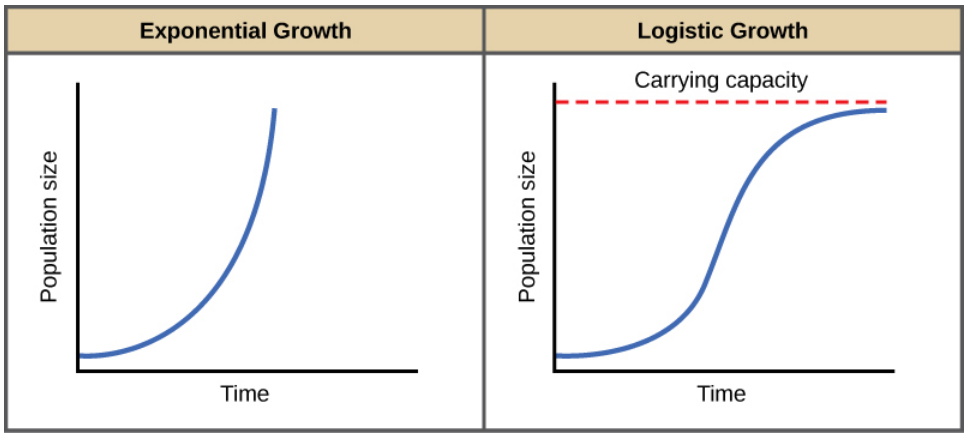


Figure 9.4.4: When resources are unlimited, populations exhibit exponential growth, resulting in a J-shaped curve. When resources are limited, populations exhibit logistic growth. In logistic growth, population expansion decreases as resources become scarce, and it levels off when the carrying capacity of the environment is reached, resulting in an S-shaped curve.

The bacteria example is not representative of the real world where resources are limited. Furthermore, some bacteria will die during the experiment and thus not reproduce, lowering the growth rate. Therefore, when calculating the growth rate of a population, the **death rate** (*D*) (number organisms that die during a particular time interval) is subtracted from the **birth rate** (*B*) (number organisms that are born during that interval). While it is not necessary for you to know the math behind this equation, it is helpful to see how ecologists utilize math to build their models. This equation for exponentially growing population is shown here:

$$\frac{\Delta N \text{ (change in number)}}{\Delta T \text{ (change in time)}} = B \text{ (birth rate)} - D \text{ (death rate)}$$

The birth rate is usually expressed on a **per capita** (for each individual) basis. Thus, *B* (birth rate) = *bN* (the per capita birth rate "*b*" multiplied by the number of individuals "*N*") and *D* (death rate) =*dN* (the per capita death rate "d" multiplied by the number of individuals "*N*"). Additionally, ecologists are interested in the population at a particular point in time, an infinitely small time interval. For this reason, the terminology of differential calculus is used to obtain the **instantaneous growth rate**, replacing the *change* in number and time with an instant-specific measurement of number and time.

$$\frac{dN}{dT} = bN - dN = (b - d)N$$

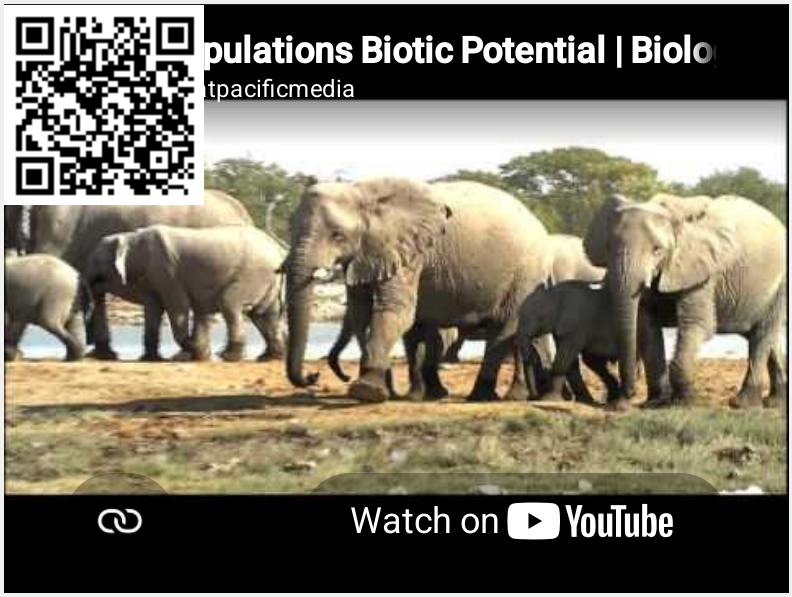
Notice that the "*d*" associated with the first term refers to the derivative (as the term is used in calculus) and is different from the death rate, also called "*d*." The difference between birth and death rates is further simplified by substituting the term "*r*" (**intrinsic rate of increase**) for the relationship between birth and death rates:

$$\frac{dN}{dT} = rN$$

The value "r" can be positive, meaning the population is increasing in size; or negative, meaning the population is decreasing in size; or zero, where the population's size is unchanging, a condition known as **zero population growth**. A further refinement of the formula recognizes that different species have inherent differences in their **intrinsic rate of increase** (often thought of as the potential for reproduction), even under ideal conditions. Obviously, a bacterium can reproduce more rapidly and have a higher intrinsic rate of growth than a human. The maximal growth rate for a species is its biotic potential, or r_{max}, thus changing the equation to:

$$\frac{dN}{dT} = r_{\max}N$$

Video



In this 3-minute video, you will be introduced to some of the factors that limit population growth.
Question after watching: What are some of the factors that may be limiting the population growth of humans? How might they act to limit population growth?

Logistic Growth

Exponential growth is possible only when infinite natural resources are available; this is not the case in the real world. Charles Darwin recognized this fact in his description of the "struggle for existence," which states that individuals will compete (with members of their own or other species) for limited resources. The successful ones will survive to pass on their own characteristics and traits (which we know now are transferred by DNA) to the next generation at a greater rate (natural selection). To model the reality of limited resources, population ecologists developed the logistic growth model.

Video



This 3-minute video will introduce you to the concept of carrying capacity.
Question after watching: Why are diseases considered a factor in carrying capacity?

Carrying Capacity and the Logistic Model

In the real world, with its limited resources, exponential growth cannot continue indefinitely. Exponential growth may occur in environments where there are few individuals and plentiful resources, but when the number of individuals gets large enough,

resources will be depleted, slowing the growth rate. Eventually, the growth rate will plateau or level off (Figure 9.4.4). This population size, which represents the maximum population size that a particular environment can support, is called the **carrying capacity**, or K.

The formula we use to calculate **logistic growth** adds the carrying capacity as a moderating force in the growth rate. The expression "K–N" is indicative of how many individuals may be added to a population at a given stage, and "K–N" divided by "K" is the fraction of the carrying capacity available for further growth. Thus, the exponential growth model is restricted by this factor to generate the logistic growth equation (again, the math is not important but seeing how the model is built is):

$$\begin{aligned}\frac{dN}{dT} &= r_{\max}\frac{dN}{dT} \\ &= r_{\max}N\frac{(K-N)}{K}\end{aligned}$$

Notice that when N is very small, $(K-N)/K$ becomes close to K/K or 1, and the right side of the equation reduces to $r_{max}N$, which means the population is growing exponentially and is not influenced by carrying capacity. On the other hand, when N is large, $(K-N)/K$ come close to zero, which means that population growth will be slowed greatly or even stopped. *Thus, population growth is greatly slowed in large populations by the carrying capacity K*. This model also allows for the population of a negative population growth, or a population decline. This occurs when the number of individuals in the population exceeds the carrying capacity (because the value of $(K-N)/K$ is negative).

A graph of this equation yields an S-shaped curve (Figure 9.4.4), and it is a more realistic model of population growth than exponential growth. There are three different sections to an S-shaped curve. Initially, growth is exponential because there are few individuals and ample resources available. Then, as resources begin to become limited, the growth rate decreases. Finally, growth levels off at the carrying capacity of the environment, with little change in population size over time.

Role of Intraspecific Competition

The logistic model assumes that every individual within a population will have equal access to resources and, thus, an equal chance for survival. For plants, the amount of water, sunlight, nutrients, and the space to grow are important resources, whereas in animals, important resources include food, water, shelter, nesting space, and mates.

In the real world, phenotypic variation among individuals within a population means that some individuals will be better adapted to their environment than others. The resulting competition between population members of the same species for resources is termed **intraspecific competition** (intra- = "within"; -specific = "species"). Intraspecific competition for resources may not affect populations that are well below their carrying capacity—resources are plentiful and all individuals can obtain what they need. However, as population size increases, this competition intensifies. In addition, the accumulation of waste products can reduce an environment's carrying capacity.

Examples of Logistic Growth

Yeast, a microscopic fungus used to make bread and alcoholic beverages, exhibits the classical S-shaped curve when grown in a test tube (Figure 9.4.5a). Its growth levels off as the population depletes the nutrients that are necessary for its growth. In the real world, however, there are variations to this idealized curve. Examples in wild populations include sheep and harbor seals (Figure 9.4.5b). In both examples, the population size exceeds the carrying capacity for short periods of time and then falls below the carrying capacity afterwards. This fluctuation in population size continues to occur as the population oscillates around its carrying capacity. Still, even with this oscillation, the logistic model is confirmed.

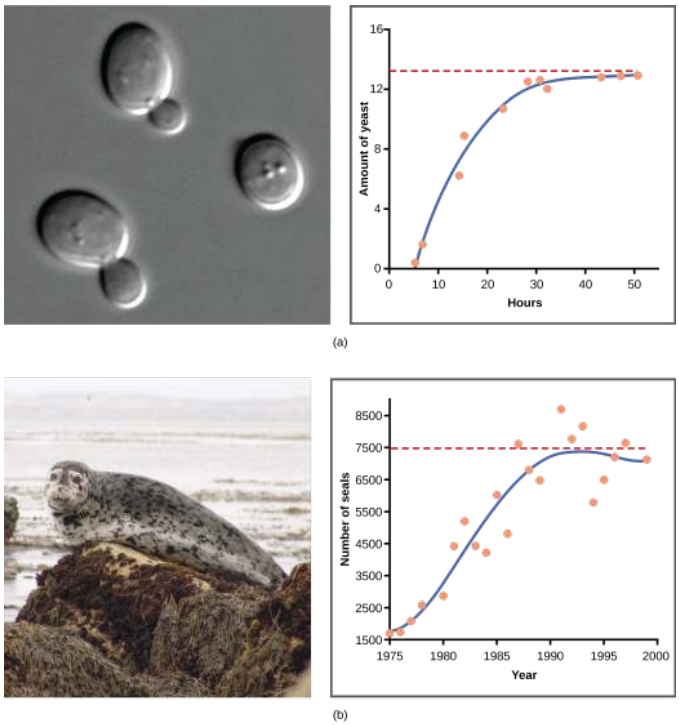
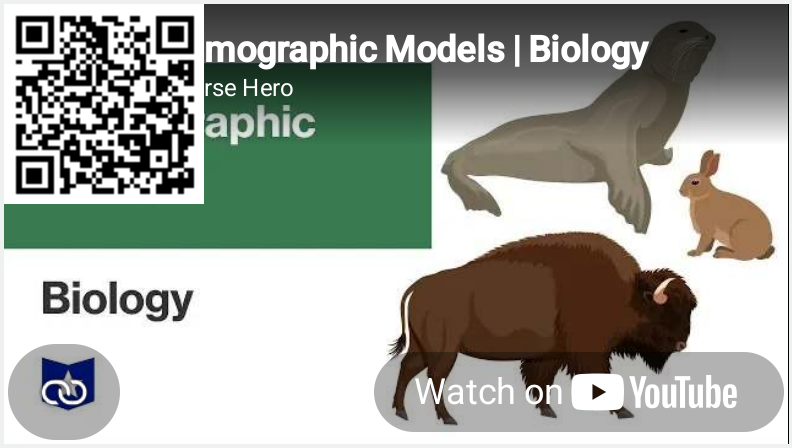


Figure 9.4.5: (a) Yeast grown in ideal conditions in a test tube show a classical S-shaped logistic growth curve, whereas (b) a natural population of seals shows real-world fluctuation.

Video



This 3-minute video reviews the various demographic models.

Question after watching: Which type of model should be applied to a perennial plant species that is introduced to a new environment without any herbivores or diseases?

Optional Activity 9.4.1

Figure 9.4.2b If the major food source of the seals declines due to pollution or overfishing, which of the following would likely occur?

A. The carrying capacity of seals would decrease, as would the seal population.
B. The carrying capacity of seals would decrease, but the seal population would remain the same.

C. The number of seal deaths would increase but the number of births would also increase, so the population size would remain the same.
D. The carrying capacity of seals would remain the same, but the population of seals would decrease.

Answer

A

Optional Activity 9.4.2

The maximum rate of growth of a species is called its _____.

a. limit
b. carrying capacity
c. biotic potential
d. exponential growth pattern

Answer

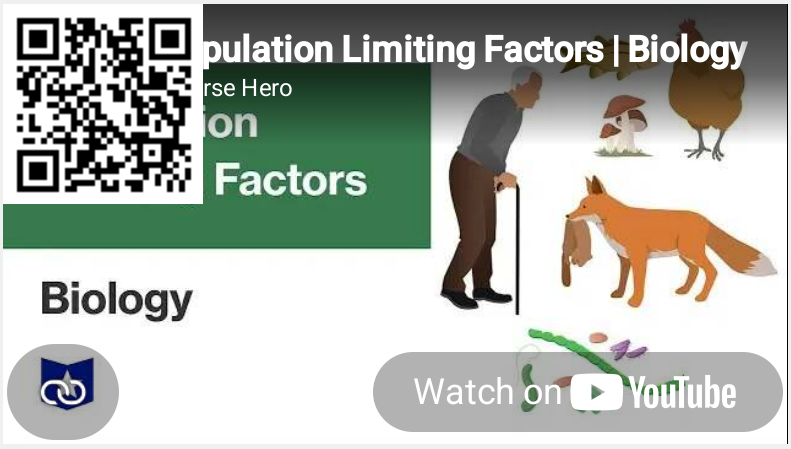
b. biotic potential

Population Limitations

The logistic model of population growth, while valid in many natural populations and a useful model, is a simplification of real-world population dynamics. Implicit in the model is that the carrying capacity of the environment does not change, which is not the case. The carrying capacity varies annually: for example, some summers are hot and dry whereas others are cold and wet. In many areas, the carrying capacity during winter is much lower than it is during summer. Also, natural events such as earthquakes, volcanoes, and fires can alter an environment and hence its carrying capacity. Additionally, populations do not usually exist in isolation. They engage in interspecific competition: that is, they share the environment with other species, competing with them for the same resources. These factors are also important to understanding how a specific population will grow.

Nature regulates population growth in a variety of ways. These are grouped into **density-dependent** factors, in which the density of the population at a given time affects growth rate and mortality, and **density-independent** factors, which influence mortality in a population regardless of population density. Note that in the former, the effect of the factor on the population depends on the density of the population at onset. Conservation biologists want to understand both types because this helps them manage populations and prevent extinction or overpopulation.

Video



In this 4-minute video, you will learn about density-dependent and density-independent factors that limit the growth of populations.

Question after watching: Disease is listed as a density-dependent factor limiting a population's growth. How might disease be density-dependent?

Density-Dependent Regulation

Most density-dependent factors are biological in nature (biotic) and include predation, inter- and intraspecific competition, stress, accumulation of waste, and diseases such as those caused by parasites. Usually, the denser a population is, the greater its mortality rate. For example, during intra- and interspecific competition, the reproductive rates of the individuals will usually be lower, reducing their population's rate of growth. In addition, low prey density increases the mortality of its predator because it has more difficulty locating its food source.

An example of density-dependent regulation is shown in Figure 9.4.6 with results from a study focusing on the giant intestinal roundworm (*Ascaris lumbricoides*), a parasite of humans and other mammals. Denser populations of the parasite exhibited lower fecundity: they contained fewer eggs. One possible explanation for this is that females would be smaller in more dense populations (due to limited resources) and that smaller females would have fewer eggs. This hypothesis was tested and disproved in a 2009 study that indicated that female weight had no influence. The actual cause of the density-dependence of fecundity in this organism is still unclear and awaiting further investigation.

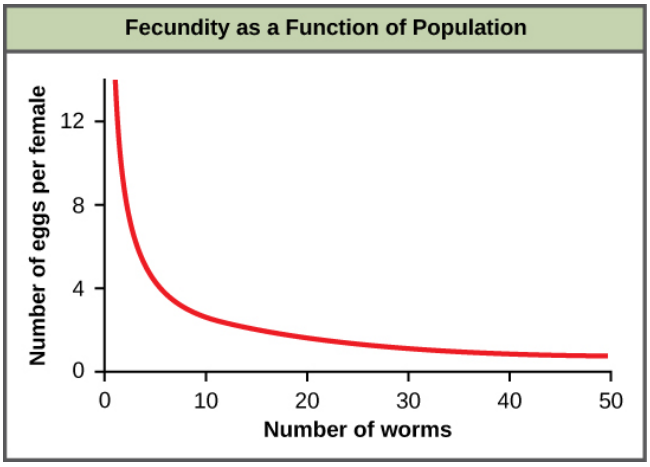


Figure 9.4.6: In this population of roundworms *Ascaris lumbricoides*, fecundity (number of eggs) decreases with population density (Croll et al. 1982).

Density-Independent Regulation

Many factors, typically physical or chemical in nature (abiotic), influence the mortality of a population regardless of its density, including weather, natural disasters, and pollution. An individual deer may be killed in a forest fire regardless of how many deer happen to be in that area. Its chances of survival are the same whether the population density is high or low. The same holds true for cold winter weather.

In real-life situations, population regulation is very complicated and density-dependent and independent factors can interact. A dense population that is reduced in a density-independent manner by some environmental factor(s) will be able to recover differently than a sparse population. For example, a population of deer affected by a harsh winter will recover faster if there are more deer remaining to reproduce.

Video



In this 2-minute video, you will explore biotic and abiotic limiting factors.

Question after watching: The video provides the example of a fish bowl and lists limiting factors on the growth of its fish population. Now apply this to a human population living in the "bowl" of a small town. List density-dependent, density-independent, biotic, and abiotic factors that will limit the human population's growth in that small town.

Optional Activity 9.4.3

Species with limited resources usually exhibit a(n) ____ growth curve.

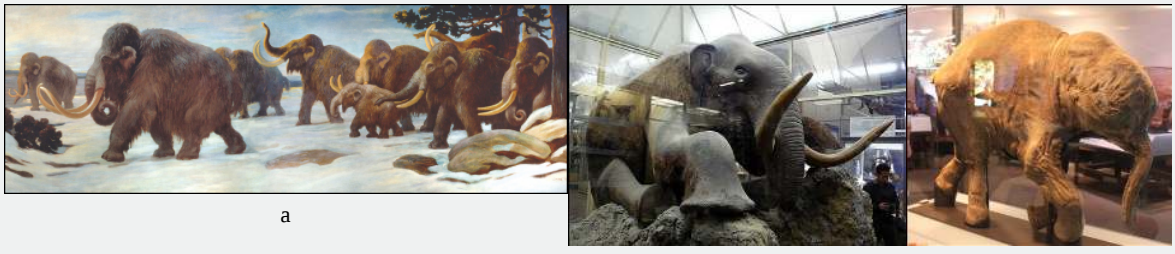
a. logistic
b. logical
c. experimental
d. exponential

Answer

a. logistic

Evolution Connection: Why Did the Woolly Mammoth Go Extinct?

It's easy to get lost in the discussion of dinosaurs and theories about why they went extinct 65 million years ago. Was it due to a meteor slamming into Earth near the coast of modern-day Mexico, or was it from some long-term weather cycle that is not yet understood? One hypothesis that will never be proposed is that humans had something to do with it. Mammals were small, insignificant creatures of the forest 65 million years ago, and no humans existed.



a b c

Figure 9.4.7: The three photos include: (a) 1916 mural of a mammoth herd from the American Museum of Natural History, (b) the only stuffed mammoth in the world, from the Museum of Zoology located in St. Petersburg, Russia, and (c) a one-month-old baby mammoth, named Lyuba, discovered in Siberia in 2007. (credit a: modification of work by Charles R. Knight; credit b: modification of work by “Tanapon”/Flickr; credit c: modification of work by Matt Howry)

Woolly mammoths, however, began to go extinct about 10,000 years ago, when they shared the Earth with humans who were no different anatomically than humans today (Figure 9.4.7). Mammoths survived in isolated island populations as recently as

1700 BC. We know a lot about these animals from carcasses found frozen in the ice of Siberia and other regions of the north like northern Canada. Scientists have sequenced at least 50 percent of its genome and believe mammoths are between 98 and 99 percent identical to modern elephants.

It is commonly thought that both climate change and human hunting led to their extinction. A 2008 study estimated that climate change reduced the mammoths' range from 8,000,000 square kilometers 42,000 years ago down to 800,000 square kilometers 6,000 years ago.[4] It is also well documented that humans hunted these animals. A 2012 study indicated that no single factor was exclusively responsible for the extinction of these magnificent creatures.[5] In addition to human hunting, climate change, and reduction of habitat, these scientists demonstrated another important factor in the mammoth's extinction was the migration of humans across the Bering Strait to North America during the last ice age 20,000 years ago.

The maintenance of stable populations was and is very complex, with many interacting factors determining the outcome. It is important to remember that humans are also part of nature. We once contributed to a species' decline using only primitive hunting technology.

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9.5: Human Population Growth

Human Population Growth

- Please read and watch the following Mandatory Resources
- Reading the material for understanding, and taking notes during videos, will take approximately ___ minutes.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Discuss how human population growth can be exponential
- Explain how humans have expanded the carrying capacity of their habitat
- Relate population growth and age structure to the level of economic development in different countries
- Discuss the long-term implications of unchecked human population growth

Concepts of animal population dynamics can be applied to human population growth. Humans are not unique in their ability to alter their environment. For example, beaver dams alter the stream environment where they are built. Humans, however, have the ability to alter their environment to increase their carrying capacity sometimes to the detriment of other species (e.g., via artificial selection for crops that have a higher yield). Earth's human population is growing rapidly, to the extent that some worry about the ability of the Earth's environment to sustain this population, as long-term exponential growth carries the potential risks of famine, disease, and large-scale death.

Although humans have increased the carrying capacity of their environment, the technologies used to achieve this transformation have caused unprecedented changes to Earth's environment, altering ecosystems to the point where some may be in danger of collapse. The depletion of the ozone layer, erosion due to acid rain, and damage from global climate change are caused by human activities. More is discussed in Unit 5. The ultimate effect of these changes on our carrying capacity is unknown. As some point out, it is likely that the negative effects of increasing carrying capacity will outweigh the positive ones—the carrying capacity of the world for human beings might actually decrease.

The world's human population is currently experiencing exponential growth even though human reproduction is far below its biotic potential (Figure 9.5.1). To reach its biotic potential, all females would have to become pregnant every nine months or so during their reproductive years. Also, resources would have to be such that the environment would support such growth. Neither of these two conditions exists. In spite of this fact, human population is still growing exponentially.

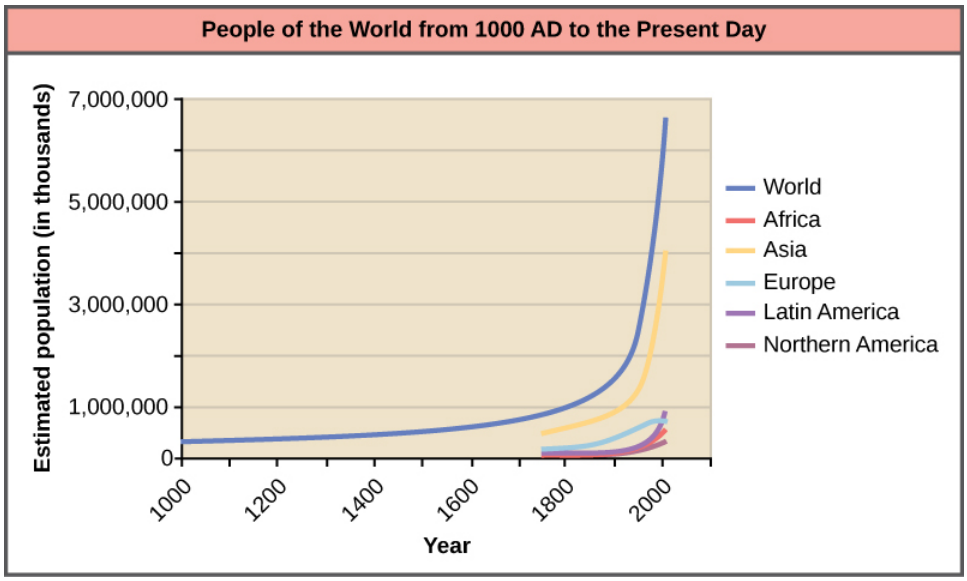


Figure 9.5.1: Human population growth since 1000 AD is exponential (dark blue line). Notice that while the population in Asia (yellow line), which has many economically underdeveloped countries, is increasing exponentially, the population in Europe (light blue line), where most of the countries are economically developed, is growing much more slowly.

A consequence of exponential human population growth is the time that it takes to add a particular number of humans to the Earth is becoming shorter. Figure 9.5.2 shows that 123 years were necessary to add 1 billion humans in 1930, but it took only 24 years to add two billion people between 1975 and 1999. As already discussed, at some point it would appear that our ability to increase our carrying capacity indefinitely on a finite world is uncertain. Without new technological advances, the human growth rate has been predicted to slow in the coming decades. However, the population will still be increasing and the threat of overpopulation remains.

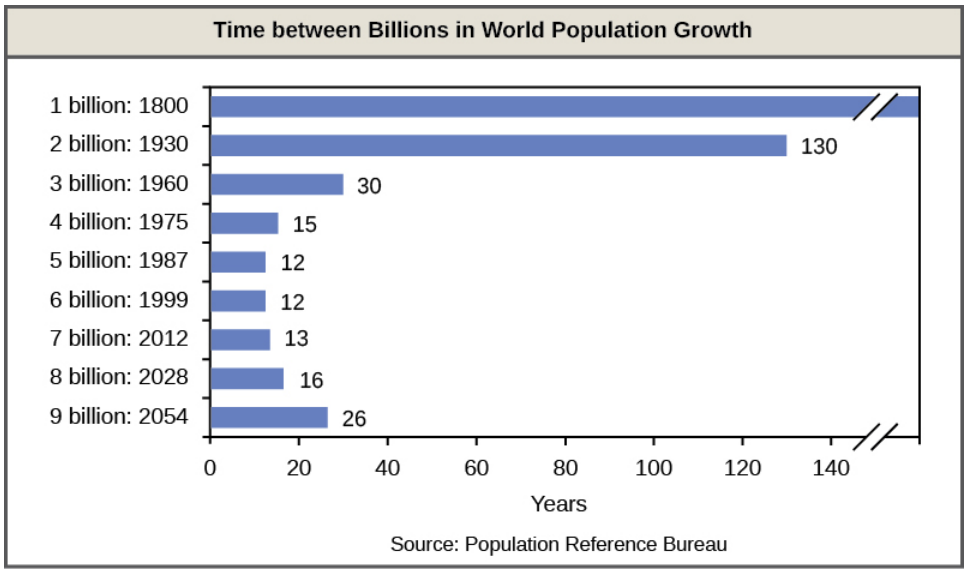
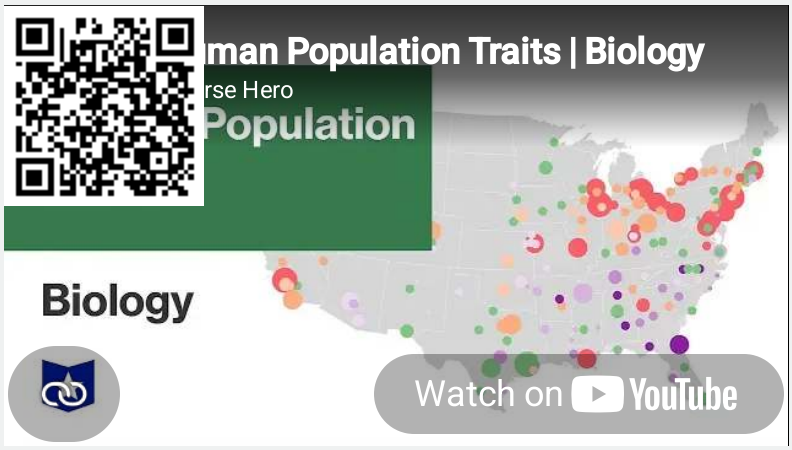


Figure 9.5.2: The time between the addition of each billion human beings to Earth decreased in 1999, and has since been increasing (indicating slowing growth). (credit: modification of work by Ryan T. Cragun)

https://bio.libretexts.org/@go/page/97680

Video



In this 4-minute video, you will explore the historical pace of human population growth.
Question after watching: Do we have an ethical obligation to limit human population growth? Why? If so, how might we do it ethically? If not, how should we distribute dwindling resources for the growing population?

Video



In this 6-minute video of the American Museum of Natural History, you will follow human population and distribution on a world map for the past 200,000 years.
Question after watching: In watching this video, what appears to have contributed to sharp rises in the human population throughout history?

Optional Activity 9.5.1

Humans have altered their own carrying capacity. Explain how humans have changed their carrying capacity and the consequences of this change.

a. By limiting their own carrying capacity, humans have enabled their population to grow rapidly.
b. By decreasing their own carrying capacity, humans have enabled their population to grow slowly.
c. By stabilizing their own carrying capacity, humans have enabled their population to grow steadily.
d. By increasing their own carrying capacity, humans have enabled their population to grow exponentially.

Answer

d. By increasing their own carrying capacity, humans have enabled their population to grow exponentially.

Overcoming Density-Dependent Regulation

Humans are unique in their ability to alter their environment with the conscious purpose of increasing its carrying capacity. This ability is a major factor responsible for human population growth and a way of overcoming density-dependent growth regulation. Much of this ability is related to human intelligence, society/culture, and communication. Humans can construct shelters to protect them from the elements and have developed agriculture and domesticated animals to increase their food supplies. In addition, humans use language to communicate this technology to new generations, allowing them to improve upon previous accomplishments.

Other factors in human population growth are migration and public health. Humans originated in Africa, but have since migrated to nearly all inhabitable land on Earth. Public health, sanitation, and the use of antibiotics and vaccines have decreased the ability of infectious disease to limit human population growth. In the past, diseases such as the bubonic plague of the fourteenth century killed between 30 and 60 percent of Europe's population and reduced the overall world population by as many as 100 million people. Today, the threat of infectious disease, while not gone, is certainly less severe. According to the World Health Organization, global death from infectious diseases declined from 16.4 million in 1993 to 14.7 million in 1992. Compared to some of the epidemics of the past, the percentage of the world's population killed between 1993 and 2002 decreased from 0.30 percent of the world's population to 0.24 percent. It appears that the influence of infectious diseases on human population growth is becoming less significant, although the SARS-CoV-2 pandemic may be a harbinger of things to come due to globalization and anti-vaccination movements.

Age Structure, Population Growth, and Economic Development

The age structure of a population is an important factor in population dynamics. Age structure is the proportion of a population at different age ranges. Age structure allows better prediction of population growth, plus the ability to associate this growth with the level of economic development in the region. Countries with rapid growth have a pyramidal shape in their age structure diagrams, showing a preponderance of younger individuals, many of whom are of reproductive age or will be soon (Figure 9.5.3). This pattern is most often observed in underdeveloped countries where individuals do not live to old age because of sub-optimal living conditions such as Mali (Stage 1). Age structures of areas with slow growth, including some developed countries such as Canada, still have a pyramidal or even arched structure, but with many fewer young and reproductive-aged individuals and a greater proportion of older individuals (Stages 2-3) (\PageIndex{4}\)). Other developed countries, such as Italy and Japan, have zero or even negative population growth. The age structure of these populations is more conical, with more middle-aged and older individuals than young people. The actual growth rates in different countries are shown in Figure 9.5.5, with the highest rates tending to be in the less economically developed countries within Africa and Asia.

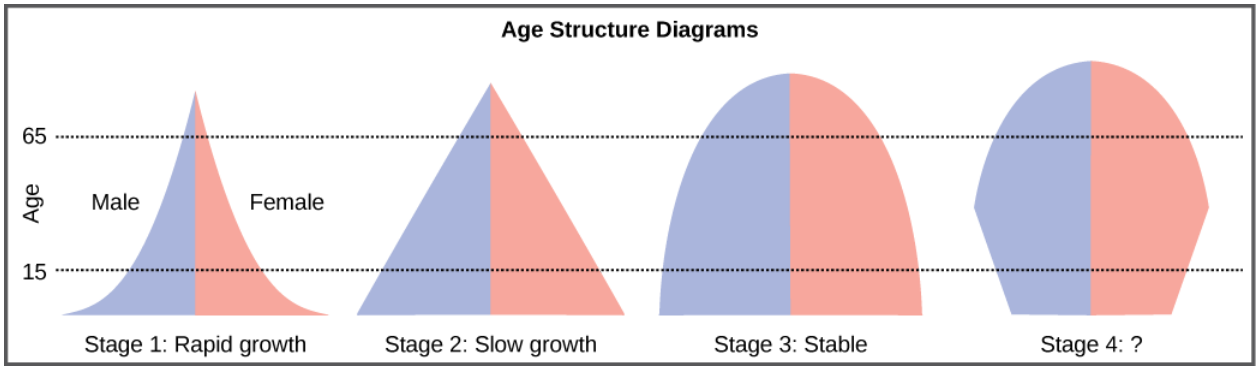


Figure 9.5.3: Typical age structure diagrams are shown. The rapid growth diagram narrows to a point, indicating that the number of individuals decreases rapidly with age. In the slow growth model, the number of individuals decreases steadily with age. Stable population diagrams are rounded on the top, showing that the number of individuals per age group decreases gradually, and then increases for the older part of the population.

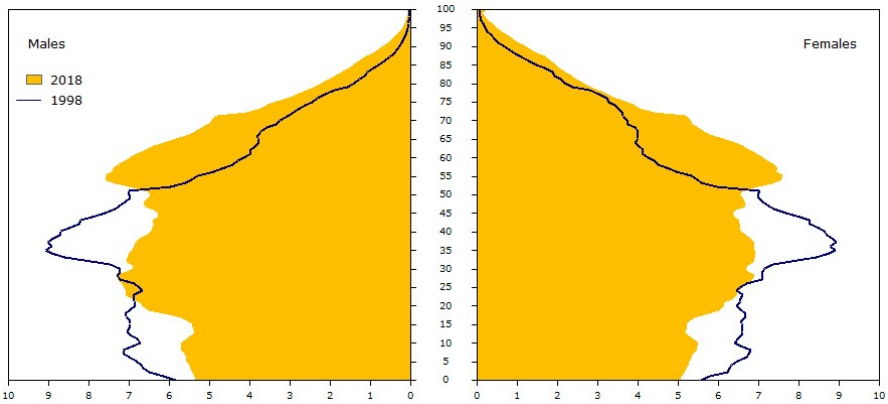


Figure 9.5.4: This graph compares the age structure of the 1998 and the 2018 population of Canada at July 1st in relative value. The left side shows males and the right side shows females. The horizontal axis shows the population in relative value and the vertical axis shows age. (Copyright 2018 Statistics Canada)

Video



In this 5-minute TED-Ed video, you will explore population statistics applied to human populations and learn to interpret the population pyramid.

Question after watching: Now that you have learned more about how to interpret a population pyramid, explain what is happening in a Stage 4 structure diagram. Which is the diagram portrayed in figure 4.2.6.3 does Canada's population fit?

Optional Activity 9.5.2

Figure 9.5.3: Age structure diagrams for rapidly growing, slow growing and stable populations are shown in stages 1 through 3. What type of population change do you think stage 4 represents?

Answer

Stage 4 represents a population that is decreasing.

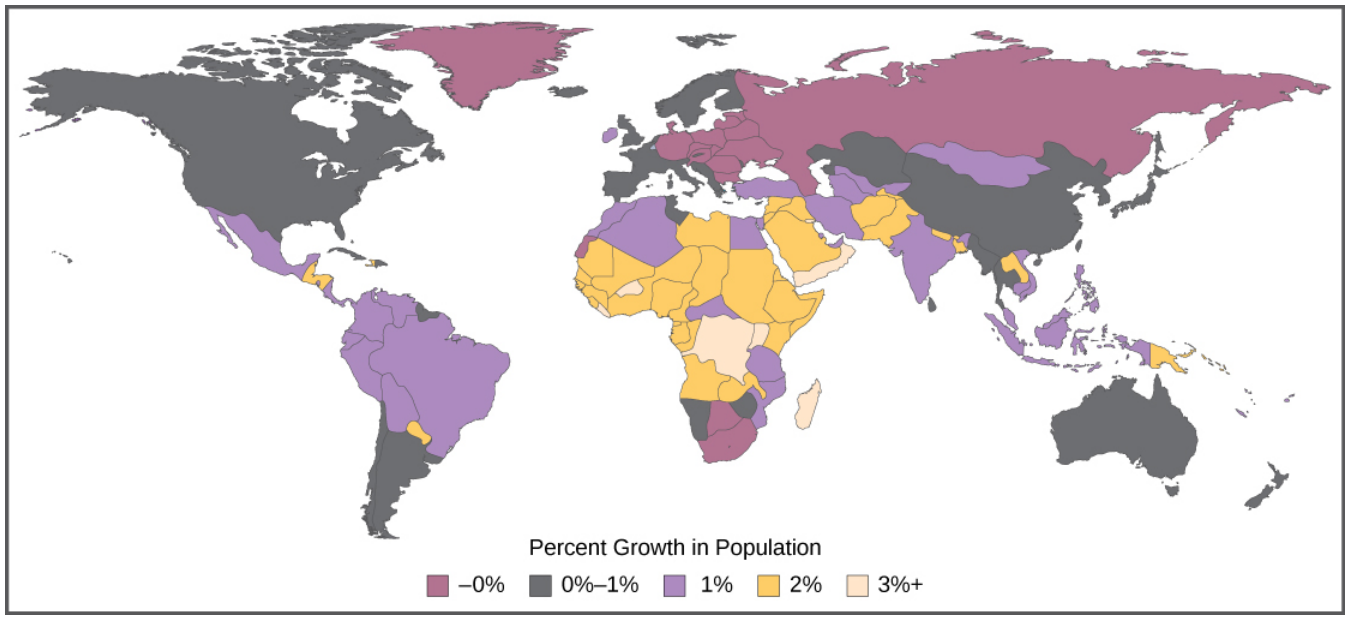


Figure 9.5.5: The percent growth rate of population in different countries is shown. Notice that the highest growth is occurring in less economically developed countries within Africa and Asia.

Long-Term Consequences of Exponential Human Population Growth

Many dire predictions have been made about the world's population leading to a major crisis called the "population explosion." In the 1968 book *The Population Bomb*, biologist Dr. Paul R. Ehrlich wrote, "The battle to feed all of humanity is over. In the 1970s hundreds of millions of people will starve to death in spite of any crash programs embarked upon now. At this late date, nothing can prevent a substantial increase in the world death rate."[1] While many critics view this statement as an exaggeration, the laws of exponential population growth are still in effect, and unchecked human population growth cannot continue indefinitely. In turn, the planet may be able to support larger numbers of humans that live with less of a collective **ecological footprint**. However, more and more individuals around the world have adopted consumerist lifestyles, and the Earth may not be able to support as many humans as it once might have been able to due to resource depletion, pollution, etc.

Video



In this 11-minute video, you will explore in more depth human population growth.
Question after watching: Water and oil are listed as essential resources for humans, over which populations fight. Would you agree that each of these is an essential resource for human populations, ones that have the potential to limit population growth? Why?

In spite of population control policies in some countries, nearly all of which have now been phased out, the human population continues to grow. At some point, food supplies may be increasingly scarce because of the subsequent need to produce more and more food to feed our population, even more challenging with the crisis of climate change. The United Nations estimates that future world population growth may vary from 6 billion (a decrease) to 16 billion people by the year 2100. There is no way to know whether human population growth will moderate to the point where the crisis described by Dr. Ehrlich will be averted.

Another result of population growth is the endangerment of the natural environment. Many countries have attempted to reduce the human impact on climate change by reducing their emissions of greenhouse gases like carbon dioxide. However, these treaties have not been ratified by every country, and many underdeveloped countries trying to improve their economic condition may be less likely to agree with such provisions if it means slower economic development. Furthermore, the role of human activity in causing climate change (Unit 5.2) has become a hotly debated socio-political issue in some developed countries. Thus, we enter the future with considerable uncertainty about our ability to curb human population growth and protect our environment.

Video



In this 10-minute video, you will learn how population geographers view human population growth.
Question after watching: In this video, you learned that many countries are encouraging populations to increase their birth rate, which is at odds with some of the data about humans having exceeded our carrying capacity on this planet. What is driving these seemingly contradictory messages?

Optional Activity 9.5.3

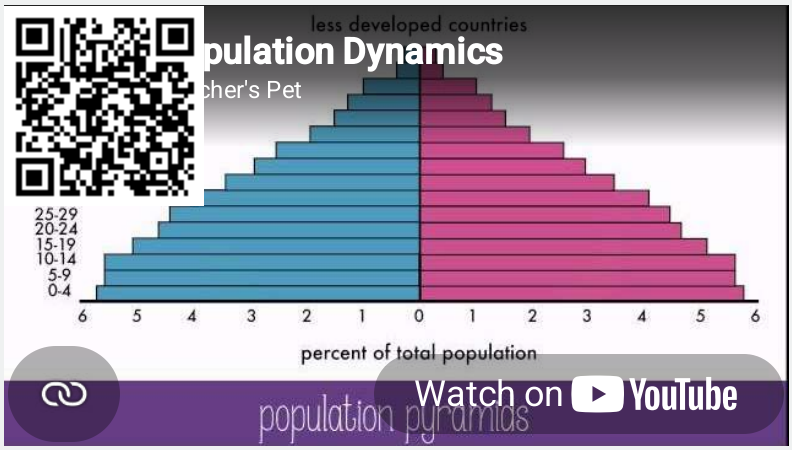
Predict and explain the effects of human population on biodiversity many years in the future.

a. Biodiversity will decline as human population increases because of habitat loss, increased pollution, and climate change.
b. Biodiversity will decline as human population increases because of enhanced food supplies, medical advances, and development of renewable energy sources.
c. Biodiversity will increase as human population increases because of habitat loss, increased pollution, and climate change.
d. Biodiversity will increase as human population increases because of enhanced food supplies, medical advances, and development of renewable energy sources.

Answer

a. Biodiversity will decline as human population increases because of habitat loss, increased pollution, and climate change.

Video



In this 4.5-minute video, you will continue to explore population dynamics. You will learn about birth and death rates and how they impact the population as a whole.

Question after watching: This video mentions that the growth rate = births - deaths. What is another factor that can impact growth rates? Why is this factor particularly important in Canada?

Footnotes

1. 1 Paul R. Erlich, prologue to *The Population Bomb*, (1968; repr., New York: Ballantine, 1970).

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CHAPTER OVERVIEW

Chapter 10: Population modeling

Learning Objectives

- Objective 1: Review the basic arithmetic and algebra needed to think quantitatively about populations using mathematical models
- Objective 2: Unpack the concept of the demographic rates of a population, including survival, birth rate, immigration, and emigration, and how these rates can be used to determine the growth rate of a population.
- Objective 3: Introduce two key patterns of population growth: exponential and logistic growth.
- Objective 4: Show how information on population growth can be used to project change in a population into the future.
- Objective 5: Detail the classic tool used by human demographers and ecologists to study population change: life tables.

10.1: Prelude - Learning the Math of Population Models

10.2: Demographic rates

10.3: Overview of Population Growth Models

10.3.1: Geometric and Exponential Growth

10.3.1.1: Logistic population growth

10.4: Projecting population growth

10.5: Life Tables

Summary

Central to population ecology is the mathematical concept -- and biological reality -- of exponential population growth. The centrality of exponential growth in ecology and evolution was recognized by Darwin and plays key role today in applied ecological decisions such as the management of invasive species, harvest limits for hunted species, and the management of endangered species. To appreciate the ecology of populations fully we therefore need to do some math. In this section, we will gently ramp up the skills and concepts we need to use math to think quantitatively about how populations change and can be effectively managed and preserved. First, we'll review the basic math we need to use throughout the chapter. Second, we'll build up the ecological concepts of demographic rates such as survival and birthrate and how they are represented mathematically. These demographic rates will then be combined into a mathematical model of population growth that shows how populations change over time due to survival and reproduction. Third, we'll show how once you have determined a population growth rate, you can predict how a population will change over time and demonstrate that it will grow exponentially. Fourth, we'll lay out a classic mathematical tool used both by human demographers and population ecologists: life tables.

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10.1: Prelude - Learning the Math of Population Models

Math and mathematical models in ecology

The processes of population changes in space and time are called **population dynamics**. Over time, a population or species may expand its geographic range, colonize a new isolated habitat patch like an island, or disappear from areas where it occurred previously (**extirpation**). Even if a population or species is only found in the same locations as previously, its population size may increase or decrease, become stable, or cycle regularly.

Ecologists frequently use **mathematical models to describe** population dynamics. These models can be used to describe the trajectory of population growth when resources are abundant, its maximum size when resources are limited, or how rapidly in space it expands into new territory. Mathematical models can be intimidating at first, but you can start learning how they work - and how to use them yourself - with the basic tools of arithmetic and algebra most people learn in high school.

Basic mathematical models can be built using algebra

The term **mathematical model** perhaps sounds fancy, but in many of their forms these are just equations manipulated using standard algebra to allow us to think about how things change. In this book we'll use models for helping us think about things like populations change over time, what impact predators have on a population of its prey, and how two species using the same resource can coexist.

Here are some examples of the level of math needed to get started working with ecological models. Elsewhere we'll investigate the applications of math in ecological modeling. Prior to studying ecology, many individuals become familiar with the equation:

$$y = M * x + B$$

This equation expresses a relationship between the **variables** x and y. In biology, we'd call this a **mathematical model** and it allows us to predict x and y for particular unknowns, such as: x is the number of birds in a population this year and y is the number next year. Or, x could be the size of a plant and y is the number of seeds it produces.

A mathematical model contains both **variables** and **parameters**. In models like ours above, x and y can be just about anything that varies between organisms or can be measured in nature: height, weight, number of species, size of a habitat, length of a river, the concentration of a toxin. In contrast, M and B are **parameters** that are generally fixed for a given situation.

Solving the variable y given x + B

Using the above equation, if I tell you $M = 1.2$ and $B = 10$, can you calculate what y is when $x = 10$? We can plug the values $M = 1.2$ and $B = 10$ into the equation:

$$y = 1.2 * x$$

We can then calculate y if $x = 10$. All the values added to the equation give us this:

$$y = 1.2 * 10 + 10$$

We then do the multiplication:

$$y = 12 + 10$$

The last step of addition tells us:

$$y = 22$$

Solving for an unknown parameter

What if I told you $y = 220$, $x = 100$, and $B = 10$; how would you calculate what M was? We could start like this with our known parameter ($B = 10$) and our values for x and y:

$$220 = M * 100 + 10$$

We then do some algebra. First deal with the 10 by subtracting it from both sides:

$$220 - 10 = M * 100 + 10 - 10$$

On the left, 220 - 10 = 210, and on the right 10 - 0 = 0, so this gives us:

$$210 = M * 100$$

Now divide both sides by 100.

$$\frac{210}{100} = \frac{M * 100}{100}$$

Which gives us:

$$\frac{210}{100} = M * 1$$

because 100/100 = 1.

Then divide 210 by 100:

$$2.1 = M$$

Not too bad? The math behind basic models in ecology is often not much more involved than this. If you can work through the steps above, you can work through the population models discussed in this book.

Using mathematical models for prediction

A common use of mathematical models in ecology is **prediction**. For example, you can often predict the number of seeds produced by a plant using an equation like this:

$$(\text{number of seeds}) = M * (\text{plant size}) + B$$

Which is the same $y = M * x + B$ equation we just used, where y = *number of seeds* and x = *plant size*.

If M = 10, B = 15, and *plant size* = 30 cm tall, how many seeds would be produced?

As before we can first add the values for the parameters M and B to to model:

$$(\text{number of seeds}) = 10 * (\text{plant size}) + 15$$

We then plug in our particular plant size of 30 cm and do the math. First multiplication:

$$(\text{number of seeds}) = 10 * 30 + 15$$

Then addition:

$$(\text{number of seeds}) = 300 + 15$$

$$(\text{number of seeds}) = 315$$

So, if the equation *(number of seeds) = 10 * (plant size) + 15* is accurate, a plant that is 30 cm tall would produce 315 seeds.

Basic population models

Population dynamics can be described with mathematical models

Populations change due to processes such as the deaths of current members of the population and the birth of new members (offspring). Discussions of population dynamics typically begin by writing out an equation which describes all of the key processes that impact population change, such as births and deaths. Most organisms live in seasonal environments, and we frequently consider changes in populations over the course of a single year, which we'll call a one-year **time step**.

Let's start building up some basic equations to describe changes in populations (**population dynamics**), calling the number of organisms right now N_{Now} and the number next year $N_{Next\ year}$ (The little "Now" and "Next year" are called **subscripts**).

We can write out how a population change like this:

$$N_{(\text{Next year})} = N_{(\text{Now})} - N_{(\text{Died this year})} + N_{(\text{Born this year})} \tag{10.1.1}$$

When we write equations like this, we always need to remember that often represent an *idealized* situation; rarely can we know how large a population currently is (N_{Now}), and it's *much* harder to determine exactly how many died or were born in a given year (We'll come back to these difficulties and their resolution in the next section on **demographic models**).

In addition to births and deaths, populations can also increase due to the arrival of individuals from different populations (**immigration)**, and decrease due to the exit of current members (**emigration)**. We therefore expand our idealized population equation to be:

$$N_{(\text{Next year})} = N_{(\text{Now})} - N_{(\text{Died this year})} + N_{(\text{Born this year})} - N_{(\text{Immigrant})} + N_{(\text{Emigrant})} \tag{10.1.2}$$

To make these equations more compact we often write using a more clearly expressed notation, where a subscript of "*t*" = a certain time, and "*t+1*" equals the following time period. Often this time step is one year, but it could be any period of time relevant to the biology of an organism or is convenient to the researcher. For example, many insects grow rapidly and some go through multiple generations in a single summer, and a relevant time step could therefore be months or even weeks.

Using subscripts we can rewrite our equation as:

$$N_{t+1} = N_t - N_{(\text{Died t})} + N_{(\text{Born t})} - N_{(\text{Immigrant t})} + N_{(\text{Emigrant t})} \tag{10.1.3}$$

where

$$N_{t+1} = N_{(\text{Next year})} \tag{10.1.4}$$

and

$$N_t = N_{(\text{Now})} \tag{10.1.5}$$

Often in textbooks births and deaths are given their own symbols, *B* and *D*, as are immigration (*I*) and emigration (*E*). You'll therefore see this equation:

$$N_{t+1} = N_t + B_t - D_t + I_t - E_t$$

or often just

$$N_{t+1} = N_t - D + B - I + E$$

with subscripts only on the N's.

Notation Alert!

Different authors and textbooks unfortunately use different notation, so it's important that everyone is clear what all their symbols mean, and that readers carefully determine what the symbols mean. In this case, it needs to be emphasized that *N*, *D*, *B*, *I*, and *E all* represent absolute numbers of individuals - they are meant to represent counts of organisms, not rates. For example, just as N_t is a count of all the individuals in the population and must be a whole number like 1000, *B* is a count of the number of births and must be a whole number like 5000. In contrast, a rate would be the number of births per individual of that population. In this case the birth rate would be *B/N* = 5000/1000 = 5. Later we will use rates, like births per year, to build demographic models.

It is useful to remember that when you're working with addition and subtraction you can move terms around in the equation and not alter the math. So our previous equation can be changed to this by **reordering** terms:

$$N_{t+1} = N_t - D + B - I + E$$

Similarly, we can add **parentheses** to help us organize things without changing the meaning. In the equation below, the number of births (B) and deaths (D) are grouped because these are opposing processes; similarly we group E (emigration) and I

(immigration). Again, this does nothing to change the meaning.

$$N_{t+1} = N_t + (B - D) + (E - I) \tag{10.1.6}$$

I can state the fact that these two equations are identical with an **equality** like this:

\[N_t + B - D + E - I = N_t + {(B - D)} + {(E - I)}

Immigration and emigration are hard to study

In the prior example, immigration and emigration were ignored. This is because immigration and emigration are *very* difficult to study in a population. Most populations are demographically **open** to immigration to some degree, especially animal populations. An **open population** is one that regularly receives immigrants from a nearby population. Only populations that occur on oceanic islands that are distant from the mainland or occur in other isolated chunks of habitat are likely to be **closed** and receive few or no immigrants.

Many habitats do have fairly rare rates of immigration, such as most islands, lakes, and isolated **fragments** of habitat that are surrounded by inhospitable conditions such as human structures. For example, Abuko Nature Preserve in The Gambia, West Africa is surrounded on all sides by the suburbs of the capital, Banjul. Except for some birds, all animals found in Abuko were born there, will live their whole lives there, and never leave. It's possible that a brave monkey may run off, but it would have to travel a considerable distance to reach the next nearest fragment of forest. For plants, most seeds will fall onto the forest floor of the preserve except those eaten by birds. These birds may happen to fly to one of the nearest forest fragments and defecate there, but it's unlikely.

Definition: Migrant

It should be noted that for human populations the general term **migrant** is often used to describe people moving to a different country. In ecology, the terms **migrant** and **migration** are often reserved for species that undergo seasonal movements between habitats.



Figure 10.1.1**:** Abuko Nature Preserve, The Gambia, West Africa. Surrounding the core forest (dark green) is more open scrub habitat (dark brown). The preserve is entirely surrounded by residences. *Source: Google Earth: https://bit.ly/abuko00*

When habitats are isolated like this, **dispersal events** are rare enough that they can be ignored for many ecological purposes. It should be noted, however, that while rare dispersal between populations doesn't have much impact on population size, it can still have an impact on **population genetics** and evolution. Population geneticists and evolutionary biologists therefore are often interested in dispersal events that a population ecologists might ignore. A population may therefore be more or less demographically closed, but **genetically open**.

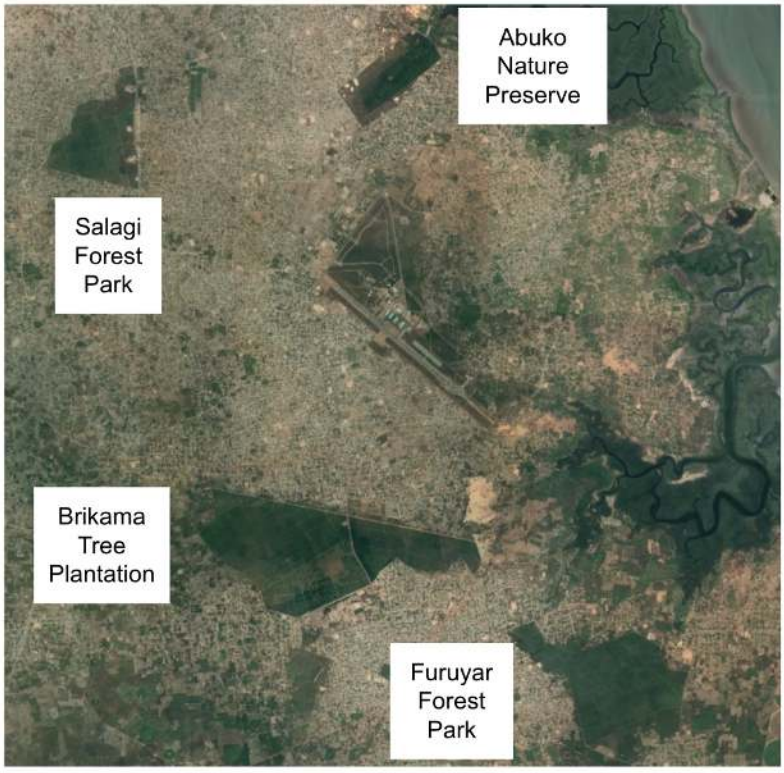


Figure 10.1.2**:** Forests nearest to Abuko Nature Preserve, The Gambia, West Africa. Most of the terrain between the forests is either residences or agricultural land. *Source:* *Google Earth: https://bit.ly/abuko1*

Ignoring immigration and emigration simplifies population models

Research on populations where immigration and emigration are minimal - or can justifiably be ignored - is convenient. This allows us to simplify our model of population dynamics from

$$N_{t+1} = N_t + B - D + E - I$$

to one without E and I:

$$N_{t+1} = N_t + B - D \tag{10.1.7}$$

We can therefore mathematically define a closed population as one where $E = 0$ and $I = 0$, and an open population as one where $E > 0$ or $I > 0$.

Moving forward, almost all of our population and other ecological models will ignore immigration and emigration. We will therefore be studying closed populations. Again, few populations are truly closed! Leaving E and I out of a model does not mean they never happen, just that they are not key players in the processes we are interested in or we are comfortable ignoring them.

While we have used a lot of symbols and equations, what we have done above presents two key creative steps in ecological modeling which are not necessarily reliant on math:

1. **Brainstorming** and writing out *all* of the key processes that can impact a population (B, D, E, I)
2. **Simplifying** the model by applying reasonable assumptions to make it easier to collect relevant data.

While math is important to the process, using your ecological imagination and intuition to determine what processes the equations should represent is just as important.

We often frame population dynamics in terms of the amount of change

Often our equation of population dynamics gets converted from focusing on the number of individuals

$$(N_t, N_{t+1}) \tag{10.1.8}$$

to the *change* in the number of individuals over time due to births and deaths. We therefore define population change as

$\Delta N = B - D$

Where is the Greek letter, Delta, which is used throughout science to mean "change."

Derivation Dance

For the curious: we can arrive at the equation $\Delta N = B - D$ via some algebra by subtracting

$$N_t \tag{10.1.9}$$

from both sides of our equation.

Our equation was:

$$N_{t+1} = N_t + B - D \tag{10.1.10}$$

We can subtract

$$N_t \tag{10.1.11}$$

from both sides:

$$N_{t+1} - N_t = N_t + B - D - N_t \tag{10.1.12}$$

Now let's rearrange terms for simplicity:

$$N_{t+1} - N_t = B - D + N_t - N_t \tag{10.1.13}$$

$$N_t - N_t = 0 \tag{10.1.14}$$

, so we simplify:

$$N_{t+1} - N_t = B - D \tag{10.1.15}$$

$$N_{t+1} - N_t \tag{10.1.16}$$

is usually written as ΔN, where is the Greek letter, Delta, which is used throughout science to mean "change".

Looking at the equation $|DeltaN = B - D$, we can ask, "*What does it mean if…*"

1. ***B* = *D*** (*B* is the same as *D*)?
2. ***B* > *D*** (*B* is *greater* than *D*)?
3. ***B* < *D*** (*B* is *less* than *D*)?

If $B = D$, the number of births is balanced out by deaths and the population has not experienced a net change in size $\Delta N = 0$. When $B > D$, births exceed deaths, ΔN is positive and the population gets bigger. When $B < D$, Δ is negative and the population gets smaller.

This all may look fairly simple if math comes easily to you, but is actually kind of profound for ecological research: you can ignore how large a population actually is and still know about its population dynamics by keeping track of just births and deaths. Conversely, if you know how much a population has changed in size, you can know whether there were more births than deaths, or if deaths exceed births. As noted before, tracking individual births and deaths is hard, so gaining insights into the net number of births and deaths just from changes in population sizes is very useful. Indeed, a whole branch of population modeling is based on this (Morris and Doak 2002).

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10.2: Demographic rates

Population dynamics are often described in terms of demographic rates

Population ecologists often collect data on **demographic rates**: **birth rates** and **death rates** (or the converse of death rate, **survival rate**). Sometimes ecologists call these **vital rates**. Formally these are called **per capita** rates because they refer to the frequency of an event per individual of the population, such as births per person. Another common way to calculate rates, though not in ecology, is **per annum.** This is the frequency of something per *year*. A model set up in terms of demographic rates is called a **demographic model**.

Study Hint

While reading about mathematical models, write out the equations and make sure you understand each step of the arithmetic and algebra.

The most direct way to collect this information is if you know *all* of the individuals in a population (N) and you can count the number of individuals that are born and which subsequently survive until they are old enough to breed. Often we call this the **birth rate**, but this is not totally correct. It should really be called the "*birth and survival until the next census period*" rate.

We'll stick with convention and call it the **birth rate** and define it like this:

$$b = (\text{birth rate}) = \frac{(\text{number of babies})}{(\text{number of adults})}$$

or more succinctly:

$$b = \frac{B_t}{N_t} \tag{10.2.1}$$

That is, the per capita birth rate b is equal to the number of births in year t (B_t) divided by the number of adults (N_t) in the population. b is a fraction, and can take on values as low as zero. $b = 0$ indicates that no offspring were born, or that all offspring died before they could reproduce. $b = 2$ indicates that two offspring were born for each adult.

Once we define b as the ratio of births to total population size, we can use algebra to set up an equation for the prediction of the actual number of births:

$$B_t = b * N_t$$

That is, the number of organisms born and entering the population at time t (B_t) is equal to the number of organisms in the population (N_t) times the number of offspring produced per organism. Stated another way, the total number born (B_t) are often expressed as a proportion (b_t) of the number alive now (N_t).

For example, at the beginning of 1996 there were 249 elephants in the Addo Elephant National Park in South Africa (Whitehouse & Hall-Martin 2000). Over the last several decades the average birth rate was 0.0693. We can therefore use our birthrate equation to predict the number of births in 1996:

$$B_{1996} = b * N_{1996} = 0.0693 * 249 = 17.25$$

Indeed, there were 17 elephants born that year.



Figure 10.2.1**:** Elephants in Addo Elephant National Park. "Elephants at the Hapoor Dam in the park" by NJR ZA is licensed by CC BY-SA 3.0.

The per capita death rate d can be similarly defined:

$$d = \frac{D_t}{N_t} \tag{10.2.2}$$

and therefore if we know the death rate and the current population size we can predict the number that will die over the next time period:

$$D_t = d * N_t$$

The mean death rate in Addo was 0.0175; 248 elephants * 0.01750 = 4.3 predicted deaths. This is slightly fewer than the 5 that actually occurred.

So far we've only been doing some minor algebraic rearrangement of these demographic rates, but seeing how this done will help us understand how to formulate demographic models for population dynamics.

Now that we're thinking in terms of rates, we can rewrite our main population dynamics equation, which was

$$N_{t+1} = N_t - D_t + B_t$$

in terms of demographic rates, like this:

$$N_{t+1} = N_t - d * N_t + b * N_t$$

What this means is that if we can estimate d and b, we can estimate population change without having to count up the total number of deaths and births.

In Addo Elephant National Park extensive data collection allowed researchers in the 1990s to account for all births, deaths, and surviving animals. However, if they had been unable to conduct a full population survey in 1997 they could've predicted the size of the population as

$$N_{1997} = N_{1996} - d * N_{1996} + b * N_{1996} = 249 - 0.0175 * 249 + 0.0693 * 249$$

This yields an estimated population size in 1997 of 262; the actual population size was 261.

Math Review

If we want, we can **factor out** the N_t from the previous equation and get an equation like this:

$$N_{t+1} = N_t + N_t * (b - d)$$

Ecologists usually calculate survival rates, not death rates

In our equations, D_t represents the *total* number of organisms that died in a given year *t*. The number that survived is therefore $N_t - D_t$.

When studying population change ecologists typically work in terms of **survival rates**, often written as ϕ, the Greek letter "Phi." The survival rate can be thought of as either a frequency or a probability. If you have 100 organisms and 50 survive to the next year, the survival rate is 0.50. Similarly, if a single organism has a 50% chance of survival over the next year, the survival rate is 0.50.

The number of deaths in a population plus the number of survivors sums to the total current population size. We therefore can use our death rate d and survival rate ϕ and write:

$$N_t = \phi * N_t + d * N_t$$

Note that in this equation we only have N_t, and not dealing right now with N_{t+1}.

We can do some algebra and move $d * N_t$ using subtraction to the left of the equals sign:

$$N_t - d * N_t = \phi * N_t$$

and see that the population size (N_t) minus those which died $(d * Nt)$ equals the number of survivors $(\phi * N_t)$.

Why all the fuss?

The previous equations aren't very profound - we're just accounting for the fate of all of the organisms currently in the population. Functioning population models, though, often rely on many basic mathematical manipulations in order to be set up, and we're taking the time to build up our intuition about how all the various pieces of these models work.

Another useful demonstration is this: we can also start as we just did with $N_t = \phi * N_t + d * N_t$ and divide both sides by N_t:

$$\frac{N_t}{N_t} = \frac{\phi * N_t + d * N_t}{N_t}$$

We can distribute the N_t on the right to give us

$$\frac{N_t}{N_t} = \frac{\phi * N_t}{N_t} + \frac{d * N_t}{N_t}$$

Nt/Nt cancels out on the left and the right. This gives us

$$1 = \phi + d$$

and by re-arrangement

$$1 - d = \phi$$

What does $1 = \phi + d$ mean? Again, mathematically it's a simple statement: the proportion which lived and the proportion which died over a single time step must total 1. However, keeping this manipulation in mind allows us to write out a demographic equation with some very useful features.

Let's put all of these pieces together. We'll start again with our key demographic equation using rates:

$$N_{t+1} = N_t - d * N_t + b * N_t$$

Next, to make this clearer we'll put related terms next to each other:

$$N_{t+1} = (N_t - d * N_t) + b * N_t$$

Now factor out N_t from the stuff in the parentheses:

$$N_{t+1} = N_t * (1 - d) + b * N_t$$

As we just showed, $1 = \phi + d$ and so our term $(1 - d)$ can be replaced like this: $1 - d = \phi$.

Therefore, we get:

$$N_{t+1} = \phi * N_t + b * N_t$$

This means that the number of individuals in the future (N_{t+1}) is comprised of those that survived $(\phi * N_t)$ and their offspring $(b * N_t)$.

In Addo Elephant National Park mean mortality was 0.0175. Mean survival is therefore 1-0.0175 = 0.9825. We therefore predict population size in the future as $N_{t+1} = 0.9825 * N_t + 0.06927 * N_t$

We've now distilled down our demographic equation to predict future population size using the present population size N_t, survival ϕ and birth rate b. While it's taken a fair bit of working with the equation, we've now reached an important breakthrough: creating a population model without determining population size at all!

Math Review

If we want to be fancy we can do a bit of algebra and factor out the N_t from the previous equation:

$$N_{t+1} = N_t * (\phi + b)$$

Let's take stock of what we've done. So far we've gone from our initial population models that show up in most biology textbooks but isn't really used by working ecologists:

$$N_{t+1} = N_t + B_t - D_t + E_t - I_t$$

and then simplified it by ignoring immigration I and emigration E, or found a population where they don't apply or can comfortably be ignored. This gives us:

$$N_{t+1} = N_t + B_t - D_t$$

Tracking total B and D is really hard -- harder than even N_t -- so we've done some simple thinking about population processes and some algebra to get:

$$N_{t+1} = \phi * N_t + b * N_t$$

where $\phi$and b are usually estimated from a subset of the population. If we are confident that our survival and birth rate estimates are good, we can predict population size in the future. However, we're still relying on estimates of population size N_t which are still costly. For example, estimating the population sizes of large animals that live in open habitats such as polar bears and elephants often requires using aircraft. For animals that live in forests it can be very difficult to determine population sizes except over small areas. In the case of plants, populations are often so large that population size can only be determined for small, isolated populations. Luckily, there are some mathematical tools we can use to build meaningful population models that don't require population sizes to be estimated. To set this type of model up we'll introduce a core concept in ecology: the population growth rate.

Population dynamics are frequently described using the population growth rate

Population ecologists are frequently interested in both the absolute number of organisms (e.g. N_t, N_{t+1}) and also the **rate of population change over time**, usually referred to as the **population growth rate**. The Greek letter "L" called "lambda" (λ) is used to represent this rate.

If you have been following a population closely over time and have complete censuses you can calculate (λ) directly using the size (N_t) of the population at one time point and at a previous time point N_{t+1}:

$$\frac{N_{t+1}}{N_t} = \lambda \tag{10.2.3}$$

λ is therefore the **ratio** between two population sizes.

In situations where population sizes have been estimated, λ can be calculated directly from these data and used in subsequent models. In other cases, demographic rates (e.g. phi and b) are used to calculate it.

Case study: Calculating lambda (λ) for Kirtland's Warbler:

The Kirtland's warbler has a small geographic range and is a habitat specialist. It therefore occurs in very specific habitats, so the approximate total number of individuals could be monitored relatively easily. In 2011 there were 1828 Kirkland's warbler males, and in 2012 there were 2090. We can therefore set up our equation with $N_t = 1828$ and $N_{t+1} = 2090$. Lambda (λ) is therefore

$$\lambda = \frac{N_{t+1}}{N_t} = \frac{N_{2012}}{N_{2011}} = \frac{2090}{1828} = 1.14 \tag{10.2.4}$$

Note that $N_{t+1} > N_t$, and therefore $\lambda > 1$.

While the warbler population grew from 2011 to 2012, the next year in 2013 only 2020 singing males were counted. Therefore

$$\lambda = \frac{N_{t+1}}{N_t} = \frac{N_{2013}}{N_{2012}} = \frac{2020}{2090} = 0.967$$

Note that $N_{t+1} < N_t$, and that $\lambda < 1$.

Once we have estimates for ϕ, we can make predictions about future population sizes and **project** population dynamics into the future. For as many years as possible, we can calculate N_{t+1}/N_t; this isn't always possible because of gaps in the data, e.g. we can't calculate N_{2014}/N_{2013} because no data was collected in 2014.

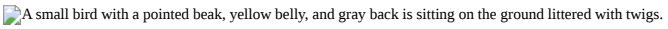


Figure 10.2.2**:** Male Kirtland's Wabler. "Kirtland" by Bjamoros is licensed under CC BY-SA 3.0.

The value of lambda summarizes population dynamics

The minimum value λ can take on is 0. When $\lambda > 1$ a population grows, while if $\lambda < 1$ a population shrinks. If $\lambda = 1$ the population isn't changing. $\lambda = 0$ means that both adult survival ϕ and reproduction b are 0. If $\lambda = 0$ the population goes extinct.

Below is a plot of the population **time series** next to a **histogram** of all of the values calculated from the time series. The time series starts in the 1970s on the left when researchers began conducting counts of all singing male Kirthland's Warblers each year. For each pair of years, λ was calculated to make the histogram.

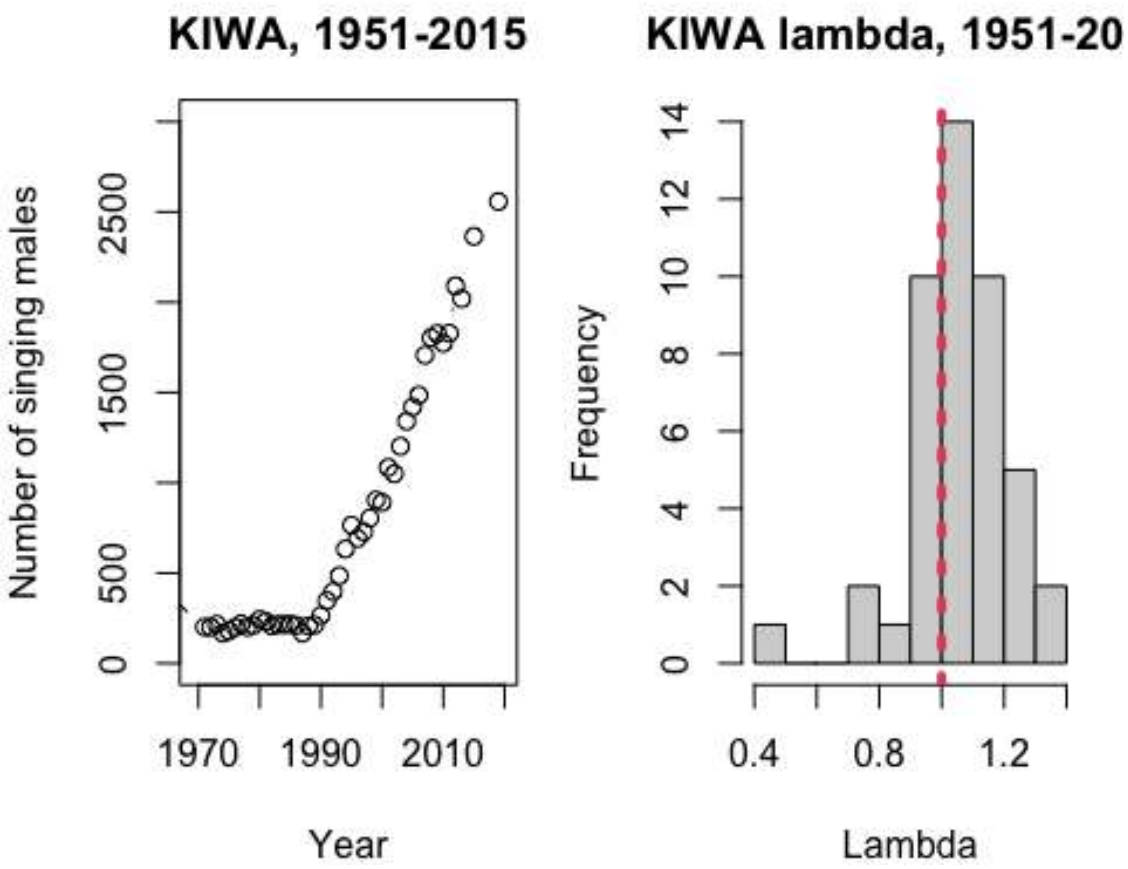


Figure 10.2.3**:** A time series (left) of the number of male Kirtland's warblers recorded and a histogram (right) of all population growth rates (λ) calculated from the time series. The histogram shows us the **distribution** of observed lambda values over the ~50 year time series when KIWA males were counted every year.

? Exercise 10.2.1

What do you notice in the KIWA Lambda histogram? Why is the red line plotted and what is happening to the population at the red line?

Answer

The red line 1.0 is plotted because when $\lambda = 1$, a population is staying the same size because deaths are being balanced out by births.

Population growth rates can be calculated from demographic rates

As noted previously, it is often very difficult – if not impossible – to determine actual population sizes. For KIWA, researchers worked very hard to determine the number of males that were singing each year, but they were never completely sure if they found all of them. KIWA population is currently growing, and researchers are no longer collecting population size data, which allows allocation of research money to answer other questions, such as the expansion of the species' range into Wisconsin and Canada.

While still very challenging, it's often easier to determine **demographic rates** for a subset of the population, such as survival and reproduction, rather than population size. Several studies have captured KIWA males, marked them with **bird bands** and attempted to re-capture them each year to estimate survival rates (ϕ). This approach for calculating survival using mark-recapture data is similar to the one discussed in the previous chapter for calculating population size. Researchers have also found nests and

determined how many baby KIWA are born per nest, and what the survival rate is for those birds until they are one year old and can breed. This gives an estimate of b.



Figure 10.2.4**:** Adult Male Kirtland's Warbler being banded. Source: Source: Hanna (2015): Kirtland's Warbler Banded as Nestling in Wisconsin Confirmed in Bahamas A Field Update. Photo by J. Trick. https://www.fws.gov/midwest/GreenBay...April2015.html

With these estimates we can calculate population growth rate (λ) without knowing population size as:

$$\frac{N_{t+1}}{N_t} = \phi + b$$

We then define N_{t+1}/N_t as λ and so have

$$\lambda = \phi + b \tag{10.2.5}$$

Derivation Dance

To show that λ can be defined with demographic rates as $\lambda = \phi + b$ we start with our previous demographic equation:

$$N_{t+1} = \phi * N_t + b * N_t$$

We can then divide both sides by Nt

$$N_{t+1}/N_t = \phi * N_t + b * N_t/N_t$$

We can distribute the division of N_t like this

$$N_{t+1}/N_t = \phi * N_t/N_t + b * N_t/N_t$$

This cancels out N_t entirely from the right-hand side

$$N_{t+1}/N_t = \phi + b$$

We then define N_{t+1}/N_t as before as

$$\lambda = \phi + b$$

λ represents a combination of both survival (ϕ) of adults from one year to the next plus how many offspring are produced per adult and survive to reproduce themselves (b). We now have a quantity we are very interested in, the population growth rate (λ), in terms of parameters that aren't too hard to calculate: the survival rate and birth rate (ϕ and b). This means we can understand population dynamics without needing to conduct a complete census and count every single organism -- just as long as we can track survival and reproduction on a representative subset of the population.

Alternative Derivation

We could also do our math this way. We can start with

$$N_{t+1} = \phi * N_t + b * N_t$$

and factor out N_t on the right to be:

$$N_{t+1} = N_t * (\phi + b)$$

We then divide both sides by N_t

$$N_{t+1}/N_t = N_t + b/Nt$$

This again gives us

$$\frac{N_{t+1}}{N_t} = \phi + b$$

which we write as

$$\lambda = \phi + b$$

Case study: Calculating Kirthland's Warbler with demographic data

We can estimate for any species if we have estimates of its adult survival rate and its birth rate. Survival for Kirtland's Warbler (KIWA) is around 67%, or 0.67. This means on average that if we have 100 adult KIWA nesting in a forest, we'd expect to see 67 of them again next year. Equivalently, we can say that an adult bird has a probability of surviving of 0.67.

The birth rate (b) is tricky to estimate for a number of reasons. Recall that b should really be called the "born and *survives* to reproduce" rate. Incorporating both the number of baby KIWA that hatch from eggs and their probability of surviving for one year until they can reproduce, the birth rate (b) is about 0.74.

Population growth rate is therefore

$$\lambda = 0.67 + 0.74$$

$$= 1.3$$

Since λ >1 we'd predict that the population of KIWA will be growing. We aren't actually counting all the birds, however.

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10.3: Overview of Population Growth Models

Skills to Develop:

By the end of this section, you will be able to do the following:

- Explain the characteristics of and differences between exponential and logistic growth patterns
- Give examples of exponential and logistic growth in natural populations
- Describe how natural selection and environmental adaptation led to the evolution of particular life history patterns

Although life histories describe the way many characteristics of a population (such as their age structure) change over time in a general way, population ecologists make use of a variety of methods to model population dynamics mathematically. These more precise models can then be used to accurately describe changes occurring in a population and better predict future changes. Certain long-accepted models are now being modified or even abandoned due to their lack of predictive ability, and scholars strive to create effective new models.

Exponential Growth

Charles Darwin, in his theory of natural selection, was greatly influenced by the English clergyman Thomas Malthus. Malthus published a book in 1798 stating that populations with unlimited natural resources grow very rapidly, which represents an **exponential growth**, and then population growth decreases as resources become depleted, indicating a logistic growth.

The best example of exponential growth is seen in bacteria. Bacteria reproduce by prokaryotic fission. This division takes about an hour for many bacterial species. If 1000 bacteria are placed in a large flask with an unlimited supply of nutrients (so the nutrients will not become depleted), after an hour, there is one round of division and each organism divides, resulting in 2000 organisms—an increase of 1000. In another hour, each of the 2000 organisms will double, producing 4000, an increase of 2000 organisms. After the third hour, there should be 8000 bacteria in the flask, an increase of 4000 organisms. The important concept of exponential growth is the accelerating **population growth rate**—the number of organisms added in each reproductive generation—that is, it is increasing at a greater and greater rate. After 1 day and 24 of these cycles, the population would have increased from 1000 to more than 16 billion. When the population size, *N*, is plotted over time, a **J-shaped growth curve** is produced (Figure 10.3.1).

The bacteria example is not representative of the real world where resources are limited. Furthermore, some bacteria will die during the experiment and thus not reproduce, lowering the growth rate. Therefore, when calculating the growth rate of a population, the **death rate (*D*)** (number organisms that die during a particular time interval) is subtracted from the **birth rate (*B*)** (number organisms that are born during that interval). This is shown in the following formula:

$$\frac{\Delta N}{\Delta T} = B - D$$

where $\Delta N =$ Change in number, $\Delta T =$ = Change in time, B = birth rate and D = death rate

The birth rate is usually expressed on a per capita (for each individual) basis. Thus, *B* (birth rate) = *bN* (the per capita birth rate "*b*" multiplied by the number of individuals "*N*") and *D* (death rate) = *dN* (the per capita death rate "d" multiplied by the number of individuals "*N*"). Additionally, ecologists are interested in the population at a particular point in time, an infinitely small time interval. For this reason, the terminology of differential calculus is used to obtain the "instantaneous" growth rate, replacing the *change* in number and time with an instant-specific measurement of number and time.

$$\frac{dN}{dT} = bN - dN = (b - d)N$$

Notice that the "*d*" associated with the first term refers to the derivative (as the term is used in calculus) and is different from the death rate, also called "*d*." The difference between birth and death rates is further simplified by substituting the term "*r*" (intrinsic rate of increase) for the relationship between birth and death rates:

$$\frac{dN}{dT} = rN$$

The value "*r*" can be positive, meaning the population is increasing in size; or negative, meaning the population is decreasing in size; or zero, where the population's size is unchanging, a condition known as **zero population growth**. A further refinement of the

formula recognizes that different species have inherent differences in their intrinsic rate of increase (often thought of as the potential for reproduction), even under ideal conditions. Obviously, a bacterium can reproduce more rapidly and have a higher intrinsic rate of growth than a human. The maximal growth rate for a species is its **biotic potential, or** r_{max}, thus changing the equation to:

$$\frac{dN}{dT} = r_{max}N$$

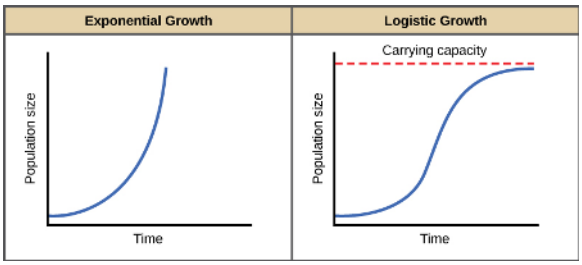


Figure 10.3.1**:** When resources are unlimited, populations exhibit exponential growth, resulting in a J-shaped curve. When resources are limited, populations exhibit logistic growth. In logistic growth, population expansion decreases as resources become scarce, and it levels off when the carrying capacity of the environment is reached, resulting in an S-shaped curve.

Logistic Growth

Exponential growth is possible only when infinite natural resources are available; this is not the case in the real world. Charles Darwin recognized this fact in his description of the "struggle for existence," which states that individuals will compete (with members of their own or other species) for limited resources. The successful ones will survive to pass on their own characteristics and traits (which we know now are transferred by genes) to the next generation at a greater rate (natural selection). To model the reality of limited resources, population ecologists developed the **logistic growth** model.

Carrying Capacity and the Logistic Model

In the real world, with its limited resources, exponential growth cannot continue indefinitely. Exponential growth may occur in environments where there are few individuals and plentiful resources, but when the number of individuals gets large enough, resources will be depleted, slowing the growth rate. Eventually, the growth rate will plateau or level off (Figure 10.3.1). This population size, which represents the maximum population size that a particular environment can support, is called the **carrying capacity, or *K***.

The formula we use to calculate logistic growth adds the carrying capacity as a moderating force in the growth rate. The expression "*K* – *N*" indicates how many individuals may be added to a population at a given stage, and "*K* – *N*" divided by "*K*" is the fraction of the carrying capacity available for further growth. Thus, the exponential growth model is restricted by this factor to generate the logistic growth equation:

$$\frac{dN}{dT} = r_{max}\frac{dN}{dT} = r_{max} * N * \frac{K-N}{K}$$

Notice that when *N* is very small, $(K-N)/K$ becomes close to K/K or 1, and the right side of the equation reduces to $r_{max}N$, which means the population is growing exponentially and is not influenced by carrying capacity. On the other hand, when *N* is large, $(K-N)/K$comes close to zero, which means that population growth will be slowed greatly or even stopped. Thus, population growth is greatly slowed in large populations by the carrying capacity *K*. This model also allows for the population of a negative population growth, or a population decline. This occurs when the number of individuals in the population exceeds the carrying capacity (because the value of $(K-N)/K$ is negative).

A graph of this equation yields an **S-shaped curve** (Figure 10.3.1), and it is a more realistic model of population growth than exponential growth. There are three different sections to an S-shaped curve. Initially, growth is exponential because there are few individuals and ample resources available. Then, as resources begin to become limited, the growth rate decreases. Finally, growth levels off at the carrying capacity of the environment, with little change in population size over time.

Role of Intraspecific Competition

The logistic model assumes that every individual within a population will have equal access to resources and, thus, an equal chance for survival. For plants, the amount of water, sunlight, nutrients, and the space to grow are the important resources, whereas in animals, important resources include food, water, shelter, nesting space, and mates.

In the real world, phenotypic variation among individuals within a population means that some individuals will be better adapted to their environment than others. The resulting competition between population members of the same species for resources is termed **intraspecific competition** (intra- = "within"; -specific = "species"). Intraspecific competition for resources may not affect populations that are well below their carrying capacity—resources are plentiful and all individuals can obtain what they need. However, as population size increases, this competition intensifies. In addition, the accumulation of waste products can reduce an environment's carrying capacity.

Examples of Logistic Growth

Yeast, a microscopic fungus used to make bread and alcoholic beverages, exhibits the classical S-shaped curve when grown in a test tube (Figure 10.3.2*a*). Its growth levels off as the population depletes the nutrients. In the real world, however, there are variations to this idealized curve. Examples in wild populations include sheep and harbor seals (Figure 10.3.2*b*). In both examples, the population size exceeds the carrying capacity for short periods of time and then falls below the carrying capacity afterwards. This fluctuation in population size continues to occur as the population oscillates around its carrying capacity. Still, even with this oscillation, the logistic model is confirmed.

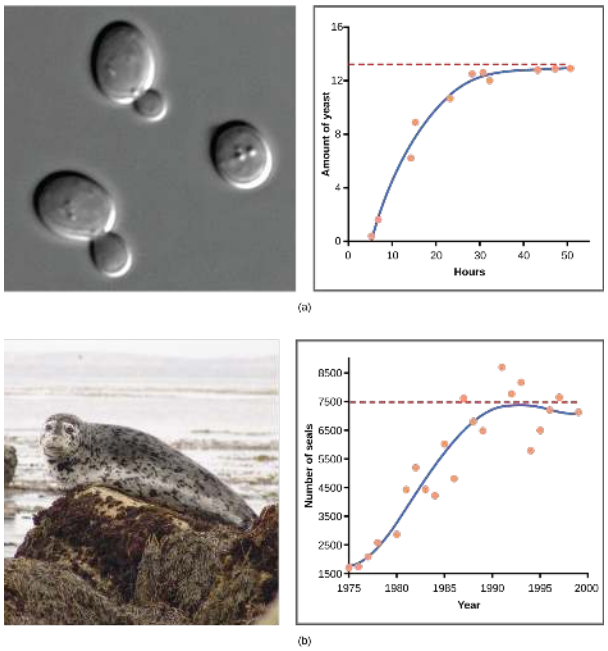


Figure 10.3.2**:** (a) Yeast grown in ideal conditions in a test tube show a classical S-shaped logistic growth curve, whereas (b) a natural population of seals shows real-world fluctuation.

? Exercise 10.3.1

If the major food source of the seals (Figure 10.3.2*b*) declines due to pollution or overfishing, which of the following would likely occur?

a. The carrying capacity of seals would decrease, as would the seal population.
b. The carrying capacity of seals would decrease, but the seal population would remain the same.

c. The number of seal deaths would increase but the number of births would also increase, so the population size would remain the same.
d. The carrying capacity of seals would remain the same, but the population of seals would decrease.

Answer

a. The carrying capacity of seals would decrease, as would the seal population.

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- OpenStax Biology 2e section 45.3 Environmental Limits to Population Growth

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10.3.1: Geometric and Exponential Growth

INTRODUCTION

We will begin by developing a population model in **discrete time**. That is, we will treat time as if it moved in steps, rather than continuously. This allows us to use difference equations rather than differential equations, and thereby avoid the calculus. This assumption is realistic for many populations that have seasonal, synchronous reproduction. Strictly speaking, the discrete-time model represents **geometric population growth**. Later in the chapter, we will develop a continuous-time model, properly called an **exponential** model.

Model Development

To begin, we can write a very simple equation expressing the relationship between population size and the four demographic processes. Let:

- N_t represent the size or density of the population at some arbitrary time t (we will ignore the distinction between population size and population density)
- N_{t+1} represent population size one arbitrary time-unit later
- B_t represent the total number of births in the interval from time t to time $t+1$
- D_t represent the total number of deaths in the same time interval
- I_t represent the total number of immigrants in the same time interval
- E_t represent the total number of emigrants in the same time interval

Then we can write

$$N_{t+1} = N_t + B_t - D_t + I_t - E_t$$

For simplicity, this exercise ignores immigration and emigration. Our equation becomes

$$N_{t+1} = N_t + B_t - D_t$$

This equation is easy to understand but inconvenient for modeling. The problem lies in the use of “raw” birth and death rates (B_t and B_t). We have no obvious, biologically reasonable starting assumptions about these numbers. However, if we switch from *raw* birth and death rates to *per capita* birth and death rates, we can do some fruitful modeling.

Geometric (Discrete-Time) Model of Population Growth

A **per capita** rate is a rate per individual; that is, the per capita birth rate is the number of births per individual in the population per unit time, and the per capita death rate is the number of deaths per individual in the population per unit time. Per capita birth rate is easy to understand, and seems a reasonable thing to model because reproduction (giving birth) is something individuals rather than whole populations do. Per capita death rate may seem strange at first; after all, an individual can die only once. But remember, this rate is calculated per unit time. You can think of per capita birth and death rates as *each individual’s probability of giving birth or dying in a given unit of time*.

Keeping in mind that per capita rates are per individual rates, we can translate the raw rates B_t and D_t into per capita rates, which we will represent with lower-case letters (b_t and d_t) to distinguish them from the raw numbers. To calculate per capita rates, we divide the raw numbers by the population size. Thus,

$$b_t = B_t/N_t \text{ and } d_t = D_t/N_t$$

Conversely,

$$B_t = b_t N_t \text{ and } D_t = d_t N_t$$

Now we can rewrite our model in terms of per capita rates:

$$N_{t+1} = N_t + b_t N_t - d_t N_t$$

Perhaps this seems to have gotten us nowhere, but it turns out to be a very informative model if we make one further assumption. Let us assume, just to see what happens, that per capita rates of birth and death remain constant over time. In other words, let us assume that average number of births per unit time per individual in the population and the average risk of dying per unit time remain unchanged over some period of time. What will happen to population size?

Because we assume *constant* per capita birth and death rates, we can make one further minor modification to our equation by leaving off the time subscripts on *b* and *d*:

$$N_{t+1} = N_t + bN_t - dN_t \tag{10.3.1.1}$$

At this point, you're probably thinking that this assumption is unrealistic—that per capita rates of birth and death *are* likely to change over time for a variety of reasons. You are quite correct, but the model is still useful for three reasons:

- It provides a starting point for a more complex and realistic model in which per capita rates of birth and death do change over time.
- It is a good *heuristic model*—that is, it can lead to insights and learning despite its lack of realism.
- Many populations *do* in fact grow as predicted by this model, under certain conditions and for limited periods of time.

Method to the madness?

You may also wonder why we use this complex model (Equation 1) rather than the simpler forms of the geometric and exponential models presented in most textbooks (and developed here beginning with Equation 2). We prefer Equation 1 for three reasons:

- It emphasizes the roles of per capita birth and death rates rather than the more abstract quantities r_d or λ (explained later).
- It allows you to manipulate per capita birth and death rates directly and separately, and discover that neither alone, but rather the difference between them, determines population growth rate.
- It allows you to discover that the per capita rate of population growth $\Delta N_t / N_t$ is a constant, which you can then relate to r_d (and r if desired).

Because per capita birth and death rates do not change in response to the size (or density) of the population, this model is said to be **density-independent**.

We can further simplify Equation 1 by factoring N_t out of the birth and death terms:

$$N_{t+1} = N_t + (b - d)N_t$$

The term (*b* – *d*) is so important in population biology that it is given its own symbol, r_d. Thus $r_d = b - d$, and is called the **geometric rate of increase**. Substituting r_d for (*b* – *d*) gives us

$$N_{t+1} = N_t + r_d * N_t \tag{10.3.1.2}$$

To further define r_d, we can calculate the amount of change in population size, ΔN_t, by subtracting N_t from both sides of Equation 2:

$$\Delta N_t = N_{t+1} - N_t = r_d N_t$$

Because $\Delta N_t = N_{t+1} - N_t$, we can simply write

$$\Delta N_t = r_d N_t \tag{10.3.1.3}$$

In words, the amount of change in population size is proportional to the population size, and the constant of proportionality is r_d.

We can convert this to per capita rate of change in population size if we divide both sides by N_t:

$$\frac{\Delta N_t}{N_t} = r_d \tag{10.3.1.4}$$

In other words, the parameter r_d represents the (discrete-time) per capita rate of change in the size of the population.

Notation note

A common source of confusion when learning about ecological is the fact that different books and other resources will use slightly different notation and alternative -- but mathematically equivalent -- ways to set up equations (**parametrizations**). For example, the source material for this chapter used R instead of r_d.

Moving on, we can simplify Equation 2 ($N_{t+1} = N_t + r_d N_t$) even further by factoring N_t out of the terms on the right-hand side, to get

$$N_{t+1} = (1 + r_d) N_t$$

The quantity $(1 + r_d)$ is often given its own symbol, λ (lambda), and its own name: the **finite rate of increase**. Substituting λ, we can write

$$N_{t+1} = \lambda N_t \tag{10.3.1.5}$$

The quantity λ can be very useful in analyzing real population data. Some additional algebra will show us how.

If we divide both sides of Equation 5 by N_t, we get

$$\frac{N_{t+1}}{N_t} = \lambda \tag{10.3.1.6}$$

In words, λ is the ratio of the population size at one time to its size one time-unit earlier. We can calculate λ from population counts at successive times, even if we do not know per capita rates of birth and death.

In Equations 2 and 5, we showed how to calculate the size of the population one time unit into the future. What if you wanted to know how big the population will be at some distant future time? You could carry out the one-time-step calculations many times, until you arrived at the desired answer. But there is also a shortcut. Population size at time 1 is $\lambda^1 N_0$, at time 2 it is $\lambda^2 N_0$, and at time 3 it is $\lambda^3 N_0$. In general, we can write

$$N_t = \lambda^t N_0 \tag{10.3.1.7}$$

Notation note

N_0 is called "N-naught." In population ecology it is often used to denote an initial population size.

Doubling time

The previous expression may strike you as rather abstract. One way to understand its impact is to use Equation 7 to calculate **doubling time** (t_{double})—that is, the time required for the population to double in size. If we plug the doubling time into Equation 7, we get

$$N_{t_{double}} = \lambda^{t_{double}} N_0$$

We can derive doubling time by exploiting the fact that the population at time t_{double} is, by definition, twice the population at time 0:

$$N_{t_{double}} = 2N_0$$

Substituting $2N_0$ for N_t double gives us

$$2N_0 = \lambda^{t_{double}} N_0$$

If we divide both sides by N_0, we get

$$2 = \lambda^{t_{double}}$$

Taking the logarithm of both sides gives us

$$ln(N_0) = t_{double} ln(\lambda)$$

Dividing both sides by $ln(\lambda)$, we get

$$\frac{ln(2)}{ln(\lambda)} = t_{double} \tag{10.3.1.8}$$

What does this mean? Suppose r_d = 0.1 individuals/individual/year. Therefore, $\lambda = 1 + r_d = 1.1$. This implies that the population increases by 10% per year, which doesn't sound like much. But, if you plug this value of λ into Equation 8, you'll find that the population doubles in about 7.27 years, which seems more impressive.

You may be wondering how a population that grows in discrete intervals of a year can double in a non-integer number of years. It can't, of course. This calculation really means that the population will not quite double in 7 years, and will more than double in 8 years.

Exponential (Continuous-Time) Model of Population Growth

Population growth can also be modeled in continuous time, which is more realistic for populations that reproduce continuously, rather than seasonally. Continuous-time models also allow use of the calculus, which provides many powerful analytical tools. Here, we will eschew the calculus, and simply present some results.

Most textbooks begin with the continuous-time analog of Equation 3:

$$dN/dt = rN \tag{10.3.1.9}$$

The left-hand side of Equation 9 represents the **instantaneous** rate of change in population size, which is different from the rate of change over some discrete time interval, $\Delta N/N$, that we looked at in Equation 7. Therefore, we use a lowercase r instead of r_d to distinguish the continuous-time exponential model from the discrete-time geometric model. The symbol r is called the **instantaneous rate of increase** or the **intrinsic rate of increase**. The parameters r and r_d are *not* equal, although they are related, as we will show below.

As we did with the discrete-time model, we can calculate the per capita rate of population growth by dividing both sides of Equation 9 by N:

$$\frac{dN/dt}{N} = r \tag{10.3.1.10}$$

You can use the calculus to operate on Equation 10 and calculate the size of the population at any time. We will spare you the derivation, but the resulting equation is

$$N_t = N_0 e^{rt} \tag{10.3.1.11}$$

where e is the root of the natural logarithms ($e \approx 2.71828$).

You can derive the relationship between r and r_d as follows. Suppose we start two populations with the same initial number of individuals, N_0, and both grow at the same rate. However, one grows in continuous time and the other grows in discrete time.

Because they grow at the same rate, at some later time, *t*, they will have reached the same size, N_t. If we write the discrete-time population on the left and the continuous-time population on the right we can derive as follows:

$$N_t = N_t$$

$$N_0\lambda^t = N_0e^{rt}$$

$$\lambda^t = e^{rt}$$

$$ln(\lambda^t) = ln(e^{rt})$$

$$tln(\lambda) = rtln(e)$$

$$ln(\lambda) = rln(e)$$

The natural log of e is 1, so

$$ln(\lambda) = r * 1$$

$$\lambda = e^r$$

So, we can convert back and forth between continuous-and-discrete time models. Remember that $\lambda = 1 + r_d$.

Suppose we have a population growing in continuous time with some value of *r*, and a population growing in discrete time with the same value of *R*, i.e., $r = r_d$. Which will grow faster? As we did with the geometric model, we can derive the doubling time for the exponential model (Gotelli 2001). We begin with Equation 11, and plug in t_double:

$$N_{t_{double}} = N_0e^{rt_{double}}$$

Substituting $2N_0$ for $N_{t_{double}}$, we get

$$2N_0 = N_0e^{rt_{double}}$$

Dividing both sides by N_0 gives us

$$2 = e^{rt_{double}}$$

and taking the natural logarithm of both sides yields

$$ln(2) = ln(e^{rt_{double}})$$

$$ln(2) = rt_{double}$$

Finally, we divide both sides by r, and rearrange, to get

$$t_{double} = \frac{ln(2)}{r}$$

Parallel to our earlier example, let us suppose $r = 0.01$ individuals/individual/year. As before, this implies a 10% annual increase in the population, but now this increase occurs continuously rather than in discrete time intervals. How long does it take for this population to double? Plugging in the value 0.1 for r yields a doubling time of 6.93 years, somewhat faster than indicated by the geometric model.

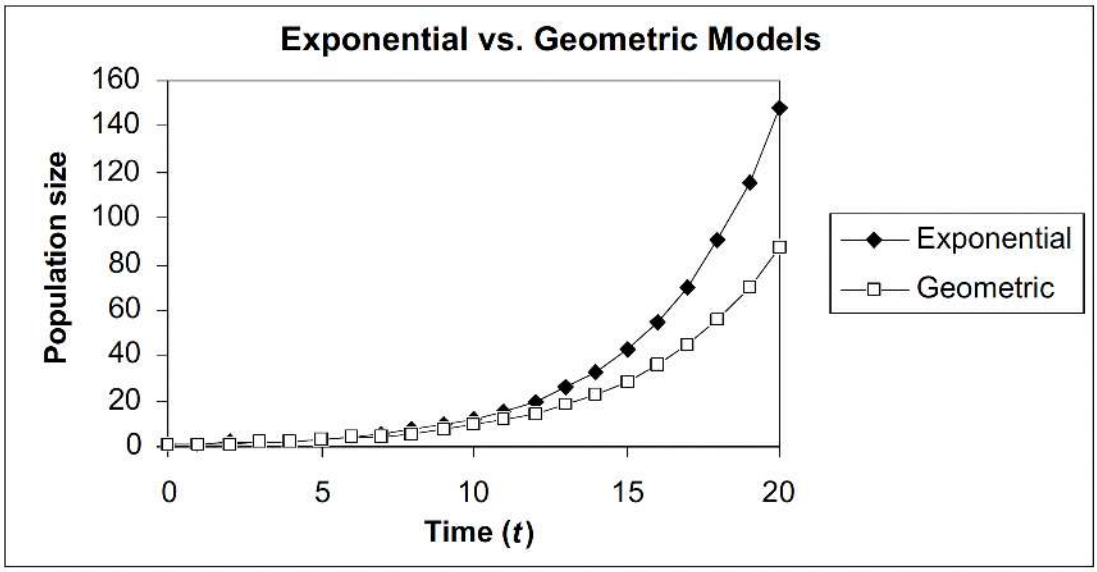


Figure 10.3.1.1**:** Exponential growth models have a faster growth rate than geometric models, so the population size of exponentially growing populations outpaces geometrically growing populations over time.

EXPLORE THIS MODEL

Before moving on to the next section, explore this Exponential Growth Shiny App developed by Dr. Aaron Howard to better understand how changes to the initial population size (N) and the population growth rate (r) impact population size over time.

References

Donovan, T.M., & Welden, C. (2002). Spreadsheet exercises in ecology and evolution. *Sinauer Associates, Inc. Sunderland, MA, USA*.

Gotelli, N.J. (2001). *A Primer of Ecology*, 3rd Edition. Sinauer Associates, Sunderland, MA.

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10.3.1.1: Logistic population growth

INTRODUCTION

This material in this chapter has been adapted from Donovan and Welden (2002).

Donovan, T. M. and C. Welden. 2002. Spreadsheet exercises in ecology and evolution. Sinauer Associates, Inc. Sunderland, MA, USA.

As in the previous section on Geometric and Exponential Growth, we begin with a model of population dynamics in discrete time, with explicit parameters for per capita rates of birth and death.

In the previous section, we developed the following geometric model of population dynamics:

$$N_{t+1} = N_t + b * N_t - d * N_t$$

where

N_t =population at time t

N_{t+1} = population at one time unit later

b= per capita birth rate

d = per capita birth rate

As you discovered in the earlier exercise, this model produces geometric population growth (the discrete-time analog of exponential growth) if b and d are held constant and $b > d$ However, the assumption that per capita rates of birth and death remain constant is unrealistic, so we will now develop a model in which these rates change. Specifically, we will consider only one cause of changes in per capita birth and death rates: the size of the population itself. In other words, we will assume that environmental conditions, food supply, and so on remain constant; only the size of the population itself changes. These additions result in the **logistic growth** model.

Because per capita rates of birth and death *do* change in response to population size or density, logistic models are **density-dependent**, in contrast to geometric and exponential models, which are density-independent. As the population grows, less food and water, fewer nesting and hiding sites, and fewer resources in general are available to each individual, affecting both an individual's rate of reproduction and its risk of death. Our model will thus include **intraspecific competition** (competition among members of the same species) for resources. These models are used to inform practical decisions in the management of fisheries and game animal populations and are used to predict the growth of the human population. Later exercises will develop models of interspecific (between two species) competition and predator-prey dynamics.

Logistic growth models include an **equilibrium population size** in this model. In other words, populations grow until they reach a stable size. The population is at equilibrium when *total* deaths equal *total* births and when *per capita* rates of birth and death are equal. This equilibrium populations size is so important in population biology, it is given its own name—the **carrying capacity**. The carrying capacity is defined as the largest population that can be supported indefinitely, given the resources available in the environment. This carrying capacity is represented by the parameter K.

$$\frac{dN}{dt} = rN\frac{(K - N_t)}{K}$$

If we begin with a very small population, the term $\frac{(K-N_t)}{K}$ is very nearly equal to $\frac{(K)}{K}$ or 1. The model will then behave like a geometric model, and the population will grow, provided $r > 1$. The population will grow slowly at first, because the parameter r is also being multiplied by a number N_t that is nearly equal to zero, but it will grow faster and faster, at least for a while. At some

point, however, population growth will begin to slow because the term $\frac{(K-N_t)}{K}$ is getting smaller and smaller as N_t gets larger and closer to K.

At the other extreme, imagine a population that starts out at a size very close to its carrying capacity, *K*. The term $\frac{(K-N_t)}{K}$ becomes nearly equal to zero, and population growth is extremely slow. When $N_t = K$, the population stops growing altogether.

EXPLORE THIS MODEL

Before moving on to the next section, explore the Logistic growth Shiny App developed by Dr. Aaron Howard to better understand how changes to the initial population size N, carrying capacity K, and the population growth rate r impact population size over time.

References

Donovan, T. M. and C. Welden. 2002. Spreadsheet exercises in ecology and evolution. *Sinauer Associates, Inc. Sunderland, MA, USA.*

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10.4: Projecting population growth

Predicting changes in population size using lambda

Once we have a value for and the current size of the population from a complete census, we can estimate the future size of the population.

Recall that we arrived at lambda previously by setting up this equation

$$N_{t+1}/N_t = \lambda = \phi + b$$

Where is ϕ the survival rate of adults, and b is the number of offspring produced per adult that live to reproduce themselves.

We can rearrange this equation for making projections like this:

$$N_{t+1} = \lambda * N_t$$

Derivation Dance

$N_{t+1}/N_t = \lambda$ indicates that our concept of lambda is based on the ratio of two population sizes. Let's start with this:

$$N_{t+1}/N_t = \lambda$$

Now multiple both sizes by N_t

$$N_{t+1}/N_t * N_t = \lambda * N_t$$

N_t cancels out from the left side and we get

$$N_{t+1} = \lambda * N_t$$

This tells us that the population size next year (N_{t+1}) can be calculated as $\lambda * (current.population.size)$.

Case Study: Projecting the number of Kirtland's Warblers

In 1990 it was estimated that there were 265 KIWA males with territories. If \[\lambda] = 1.3 as we calculated earlier, we'd predict that in 1991 the population size would be

$$N_{1991} = \lambda * N_{1990}$$

$$N_{1991} = 1.3 * 265 = 344.5$$

So we'd predict there to be 344 or 345 birds in 1991 (you can't have 0.5 of an organism. Indeed, researchers observed 347 birds.

We can repeat this using our estimate for 1991 to estimate 1992 and so on. When you plug the output of an equation (eg N_{1991}=344) back into itself repeatedly this is called **recursion.**

The equation

$$N_{t+1} = \lambda * N_t$$

is therefore sometimes referred to as a **recursion equation**. (Similar terms are **iterate** and **iteratively**.)

Exponential population growth

If you take the population size of 344 KIWA from our last calculation and plug it back into the population growth equation like this to estimate the number of warblers in the next year, 1992:

$$N_{1992} = 1.3 * 344 = 447.2$$

The estimated population the following year will be about 447 KIWA males. In reality, there were 497 males counted, so our projection is a bit low

If you repeat this process of plugging the results of one calculation into the next calculation 8 more times (for 10 total years of population change) we can project the population size for a decade. Note the convex, upward curvature of the line. This upward, accelerating curve is an **exponential growth curve**. Exponential growth occurs when something increases by multiplication. This is in contrast to **arithmetic growth**, which occurs when something increases by addition.

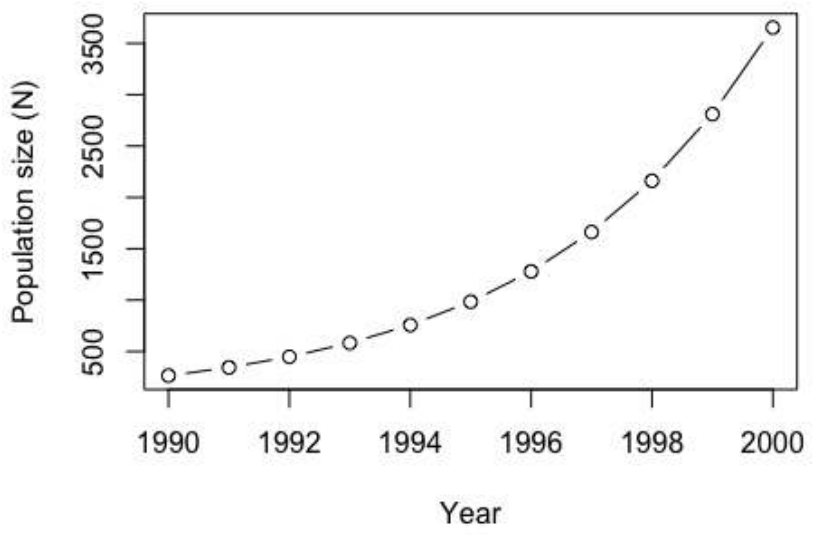


Figure 10.4.1**:** Exponential growth increases by multiplication and accelerates the population size over time without limit.

Many things in the world change arithmetically. For example, if you are being paid by the hour to do a job and don't have to work an entire day, the amount you earn increases arithmetically. Some populations can grow arithmetically if individuals from other populations are being **introduced** intentionally to the population. For example, the Peregrine falcon (*Falco peregrinus*) has a geographic range that encompases the entire world. However, due to the impacts of pesticides such as DDT the falcon was almost extirpated from many places in the United States. In addition to banning DDT, falcon populations were restored by taking young falcons from large populations and introducing them to smaller populations. If 10 falcons were introduced each year to a population, the fixed number of new individuals results in arithmetic contribution to growth.

In contrast to the fixed increases of arithmetic growth, exponential growth occurs multiplicatively - that is, by multiplying the current population size by a growth rate. If a population of falcons has 100 birds and a growth rate of 1.10, then it's population size the next year is 100*1.10 = 110. The next year if the growth rate is still 1.10 the population would be 110*1.10 = 121. Therefore the first time step the change in population size (delta N) was 10 individuals (110-100 = 10), while over the second time step delta N was 11 individuals (121-110 = 11). If we projected a third year the population would be 121*1.10 = 133.1. Delta N is therefore increasing each year from 10, to 11, to about 12. This is why we use the term "*accelerating*" to describe this type of growth: each year the amount of change increases.



Figure 10.4.2**:** Male peregrine falcon (*Falco peregrinus*) in Humber Bay Park West in Toronto. "*Falco peregrinus*" by Сапсан is licensed under CC BY-SA 3.0.

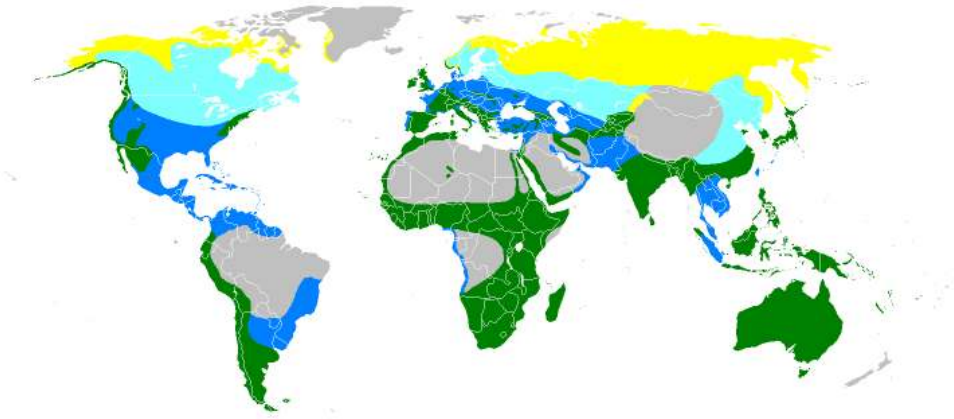


Figure 10.4.3**:** The peregrine falcon's range covers most of the world, besides some areas of Africa, the Arabian Peninsula, South America, Greenland, and Asia. The birds' large home range allows for alternative options from limiting factors. "Range map for *Falco peregrinus* (including *F. (p.) pelegrinoides*, the Barbary falcon)" by MPF is licensed under CC BY-SA 3.0.

Case study: The Montserrat Oriole

The Montserrat Oriole (*Icterus oberi*) is a relative of the Baltimore Oriole (*Icterus galbula*). While the Baltimore Oriole occurs throughout eastern and central North America, the Montserrat Oriole lives only on the Caribbean island of Montserrat. Montserrat is a small volcanic island that is only about 10 miles long and 7 miles wide and lies east of Puerto Rico and north of Barbados. Since the Montserrat Oriole only occurs on the island of Montserrat. It therefore is an entirely closed population. The Montserrat Oriole is therefore called a single-island **endemic species**, like the Cozumel Thrasher.



Figure 10.4.4**:** The red box identifies Montserrat. "Location of Montserrat" by TUBS is licensed under CC BY-SA 3.0 / adapted from original.



Figure 10.4.5**:** The Montserrat Oriole is only present on the island of Montserrat in a closed population. "Male Montserrat Oriole (*Icterus oberi*), London Zoo" by Neil Phillips is licensed under CC BY 2.0.

Volcanic activity in the 1990s on Montserrat has destroyed its forest habitat and rained ash down across the island, destroying nests and killing the birds' insect prey. N was therefore negative due to a low number of births of new birds and a high death rate of members of the existing population due to starvation. The species is therefore threatened with **extinction** - death of all members of the population. Biologists have become very interested in determining how many orioles are left on the island and what is happening with the population.

The Montserrat Oriole population size is small, but researchers have never been able to determine how many there are. What they have done, however, is marked a subset of adult orioles with **bird bands** and re-captured them each year to estimate survival rates. They have also found some nests and determined how many baby orioles are born per nest, and what the survival rate is for those birds until they are one year old and can breed. This gives an estimate of b.

Survival for the Montserrat Oriole is currently around 70%, or 0.70. This means that if there were 100 birds banded, 70 of them survived to the following year. Alternatively, we can think of this in terms of probability: a single bird banded this year has a 70% chance of surviving to the next year to be re-captured.

The birth rate is tricky to estimate for a number of reasons; incorporating both the number of Orioles that hatch from eggs and their probability of surviving for one year until they can reproduce, the birth rate (b) is about 0.42. The population growth rate is therefore

$$\lambda = 0.70 + 0.42$$

$$\lambda = 1.12$$

Since λ >1 we'd predict that the population of Orioles will be growing. As before, we aren't actually counting all the birds, but instead using demographic rates to estimate lambda.

In 2012 it was estimated that there might be as few as 300 Orioles on the island. If $\lambda = 1.12$ as we calculated above, we'd predict that in 2013 the population size would be

$$N_{2013} = \lambda * N_{2012}$$

$$N_{2013} = 1.12 * 300 = 336$$

In 2001 a second, very small population of Montserrat Orioles was found very near to the crater of the volcano on the island. Researchers haven't studied this population much, but they estimate that there were about 100 birds in 2020.



Figure 10.4.6**:** Green spots on the island of Montserrat identify habitats. "Range map of Montserrat Oriole (*Icterus oberi*)" by Cephas is licensed under CC BY-SA 4.0.

If you start with 100 Orioles and you estimate that for this population is 1.10 you can start with this equation

$$N_{t+1} = \lambda * Nt$$

We can make this more specific with subscripts:

$$N_{2021} = \lambda * N_{2020}$$

then plug in the values $lambda = 1.10$ and N = 100

$$N_{2021} = 1.1 * 100$$

and get the project population the following year

$$N_{2021} = 110$$

So, if you have 100 orioles in 2020 you'd expect to have 2021 next year.

Exponential population growth of Orioles

If you take the population size of 110 orioles from our last calculation and plug it back into the population growth equation you can estimate the number of orioles in next year, 2022:

$$N_{2022} = 1.1 * 110$$

the estimated population the following year will be 121 orioles.

$$N_{2022} = 121$$

If you repeat this 8 more times (for 10 total years of population change since 2020) you will see a graph like the one below. Note the slight, convex, upward curvature of the line.

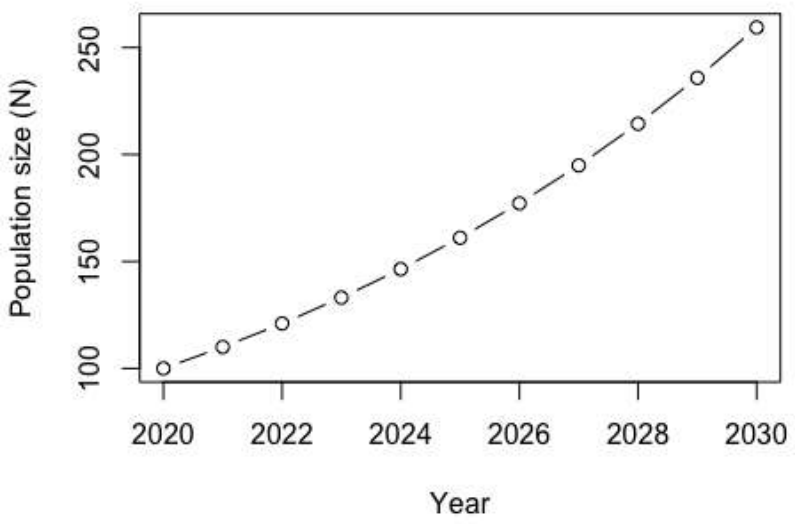


Figure 10.4.7**:** Exponential growth models can be used to graph the predicted population sizes of species.

Contributors and Attributions

This chapter was written by NL Brouwer (University of Pittsburgh)

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10.5: Life Tables

This material in this chapter has been adapted from Donovan and Welden (2002).

Donovan, T. M. and C. Welden. 2002. Spreadsheet exercises in ecology and evolution. Sinauer Associates, Inc. Sunderland, MA, USA.

Objectives

- Use age or stage-specific abundance data to calculate a variety of life table parameters.
- Discover how patterns of survivorship relate to the classic three types of survivorship curves.
- Learn how patterns of survivorship relate to life expectancy.
- Explore how patterns of survivorship and fecundity affect the rate of population growth.

10.5.1: Introduction

A life table is a record of survival and reproductive rates in a population, broken out by age, size, or developmental stage (e.g., egg, hatchling, juvenile, adult). Ecologists and demographers (scientists who study human population dynamics) have found life tables useful in understanding patterns and causes of mortality, predicting the future growth or decline of populations, and managing populations of endangered species.

Predicting the growth and decline of human populations is one very important application of life tables. As you might expect, whether the population of a country or region increases or decreases depends in part on how many children each person has and the age at which people die. But it may surprise you to learn that population growth or decline also depends on the age at which they have their children.

Another use of life tables is in species conservation efforts, such as in the case of the loggerhead sea turtle of the southeastern United States (Crouse et al., 1987). Generally speaking, the loggerhead population is declining and mortality among loggerhead eggs and hatchlings is very high. These facts led conservation biologists to advocate for the protection of nesting beaches. When these measures proved ineffective in halting the population decline, compiling and analyzing a life table for loggerheads indicated that reducing mortality of older turtles would have a greater probability of reversing the population decline. Therefore, management efforts shifted to persuading fishermen to install turtle exclusion devices on their nets to prevent older turtles from drowning.

10.5.2: **Life Table Varieties**

Life tables come in two varieties: cohort and static. A **cohort life table** follows the survival and reproduction of all members of a cohort from birth to death. A cohort is the set of all individuals born, hatched, or recruited into a population during a defined time interval. Cohorts are frequently defined on an annual basis (e.g., all individuals born in 1978), but other time intervals can be used as well.

A **static life table** records the number of living individuals of each age in a population and their reproductive output. The two varieties have distinct advantages and disadvantages, some of which we discuss below.

Life tables (whether cohort or static) that classify individuals by age are called **age-based life tables**. Such life tables treat age the same way we normally do: that is, individuals that have lived less than one full year are assigned age zero; those that have lived one year or more but less than two years are assigned age one; and so on. Life tables represent age by the letter x, and use x as a subscript to refer to survivorship, fecundity, and so on, for each age.

Size-based and **stage-based life tables** classify individuals by size or developmental stage, rather than by age. Size-based and stage-based tables are often more useful or more practical for studying organisms that are difficult to classify by age, or whose

ecological roles depend more on size or stage than on age.

10.5.2.1: Cohort Life Tables

To build a cohort life table for, let's say, humans born in the United States during the year 1900, we would record how many individuals were born during the year 1900, and how many survived to the *beginning* of 1901, 1902, etc., until there were no more survivors. This record is called the **survivorship schedule**.

We must also record the **fecundity schedule**—the number of offspring born to individuals of each age. The total number of offspring is usually divided by the number of individuals in the age, giving the average number of offspring per individual, or per capita fecundity.

Many life tables count only females and their female offspring; for animals with two sexes and equal numbers of males and females of each age, the resulting numbers are the same as if males and females were both counted. For most plants, hermaphroditic animals, and many other organisms, distinctions between the sexes are nonexistent or more complex, and life table calculations may have to be adjusted.

10.5.2.2: Static Life Tables

A static life table is similar to a cohort life table but introduces a few complications. For many organisms, especially mobile animals with long life spans, it can be difficult or impossible to follow all the members of a cohort throughout their lives. In such cases, population biologists often count how many individuals of each age are alive *at a given time*. That is, they count how many members of the population are currently in the 0–1- year-old class, the 1–2-year-old class, etc.

These counts can be used as if they were counts of survivors in a cohort, and all the calculations described below for a cohort life table can be performed using them. In doing this, however, the researcher must bear in mind that she or he is assuming that age-specific survivorship and fertility rates have remained constant since the oldest members of the population were born. This is usually not the case and can lead to some strange results, such as negative mortality rates. These are often resolved by averaging across several ages, or by making additional assumptions.

10.5.3: **Life Table Parameters**

Survivorship and fecundity schedules are the raw data of any life table. From them we can calculate a variety of other quantities, including age-specific rates of survival, mortality, fecundity, survivorship curves, life expectancy, generation time, net reproductive rate, and intrinsic rate of increase. Which of these quantities you calculate will depend on your goals in constructing the life table.

Key Parameters

x and n_x When conducting a study, these are the data generally collected on populations. We then calculate the rest of the life table from these data.

- x The first column, represents the age classes. This column could represent days, minutes, or life stages (eggs, juveniles, adults, etc.).
- n_x The number of individuals from the original cohort that are alive at the specified age, age class, or life stage (x).

From information on the number of individuals at each age, we can calculate a variety of survival and mortality rates.

- d_x The difference between the number of individuals alive for any age class (n_x) and the next older age class (n_{x+1}) is the number of individuals that have died during that time intervals. d_x is a measure of age-specific mortality.
- q_x The number of individuals that died during any given time interval (d_x) divided by the number alive at the beginning of that interval (n_x) provides an age-specific mortality rate.

- s_xThe age-specific survival rate for age interval x is the proportion of individuals that survive during any given time interval.
- l_x The number of individuals surviving to any given life stage as a proportion of the original cohort size. l_x represents the probability at birth of surviving to any given life stage.

Calculating life expectancy E_x requires calculating two additional parameters, L_x and T_x.

- L_x The number of individuals that are alive in the middle of the first age class – 0.5 years old, or 1.5 years old.
- T_x The total years lived into the future by individuals in age class x. This value is calculated by summing the values of Lx cumulatively from age x to the end of the life table. The number of time units left for all individuals to live from age x onward – obtained by summing all values of L_x.
- E_x The life expectancy for an individual of age x is age-specific life expectancy divided by number of individuals at age x. Life expectancy represents the average additional length of times than an individual will live once it has reached age x.

A typical life table is shown in Figure 1. If we were to build a cohort life table for a population born during the year 1900, we would record how many individuals were born during the year 1900, and how many survived to the *beginning* of 1901, 1902, etc., until there were no more survivors. This record is called the **survivorship schedule**. We would also record the **fecundity schedule**: the number of offspring born to members of each age class. The total number of offspring is usually divided by the number of individuals in the age class, giving the average number of offspring per individual, which is represented by b_x.

	A	B	C	D	E	F
1	Cohort Life Table: Fecundity Schedule and Population Growth					
2						
3	Age class (x)	S_x	b_x	l_x	$(l_x)(b_x)$	$(l_x)(b_x)(x)$
4	0	3751	0.00	1.0000	0.0000	0.0000
5	1	357	10.51	0.0952	1.0003	1.0003
6	2	159	0.00	0.0424	0.0000	0.0000
7	3	59	0.00	0.0157	0.0000	0.0000
8	4	57	0.00	0.0152	0.0000	0.0000
9	5	53	0.00	0.0141	0.0000	0.0000
10	6	29	0.00	0.0077	0.0000	0.0000
11	7	19	0.00	0.0051	0.0000	0.0000
12	8	17	0.00	0.0045	0.0000	0.0000
13	9	13	0.00	0.0035	0.0000	0.0000
14	10	7	0.00	0.0019	0.0000	0.0000
15	11	0		0.0000	0.0000	0.0000
16				Total	1.0003	1.0003
17	R_0	1.0003				
18	G	1.0000				
19	r est.	0.0003				

Figure 10.5.1**:** A cohort of 3751 individuals tracked over time. The number alive at the beginning of each year is given in Column B, and the average number of offspring per female is given in Column C. Columns D through G are calculated from information in columns A through C.

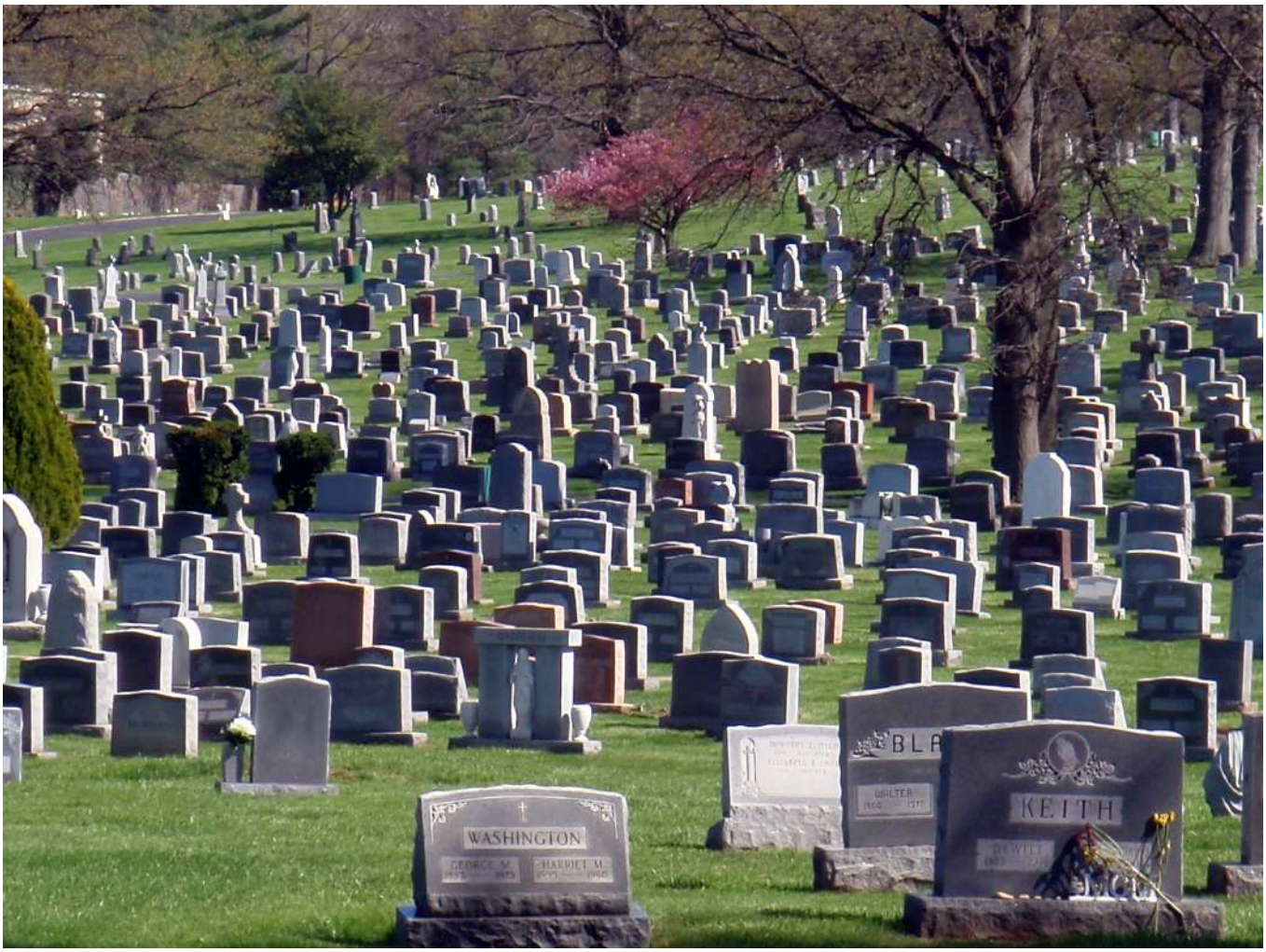


Figure 10.5.2**:** "Mt. Olivet Cemetery" was taken by Daniel Lobo and is licensed under Creative Commons Attribution 2.0 Generic.

Calculating Key Parameters

Standardized Survival Schedule (l_x). Because we want to compare cohorts of different initial sizes, we standardize all cohorts to their initial size at time zero, n_0. We do this by dividing each n_x by n_0. This proportion of original numbers surviving to the beginning of each interval is denoted l_x, and calculated as

$$l_x = \frac{n_x}{n_0} \tag{10.5.1}$$

We can also think of l_x as the probability that an individual survives from birth to the beginning of age x. Because we begin with *all* the individuals born during the year (or other interval), l_x always begins at a value of one (i.e., n_0/n_0), and can only decrease with time. At the last age, k, n_k is zero.

Age-Specific Survivorship (S_x)**.** Standardized survivorship, l_x, gives us the probability of an individual surviving from birth to the beginning of age x. But what if we want to know the probability that an individual who has already survived to age x will survive to age $x+1$? We calculate this age-specific survivorship as $S_x = l_{x+1}/l + x$, or equivalently,

$$S_x = \frac{n_{x+1}}{n_x} \tag{10.5.2}$$

Life Expectancy (E_x)**.** You may have heard another demographic statistic, life expectancy, mentioned in discussions of human populations. Life expectancy is how much longer an individual of a given age can be expected to live beyond its present age. Life expectancy is calculated in three steps.

First, we compute the proportion of survivors at the mid-point of each time interval (L_x—note the capital L here); that is,

$$L_x = \frac{n_x + n_{x+1}}{2} \tag{10.5.3}$$

Second, we sum all the L_x values from the age of interest (n) up to the oldest age, k:

$$T_x = \sum_{n=1}^{\infty}(L_x) \tag{10.5.4}$$

Finally, we calculate life expectancy as

$$E_x = \frac{T_x}{n_x} \tag{10.5.5}$$

Life expectancy is age-specific—it is the expected number of time-intervals remaining to members of a given age. The statistic most often quoted (usually without qualification) is the life expectancy at birth (E_0).

10.5.4: Survivorship Curves

There are three classic survivorship curves, called Type I, Type II, and Type III (Figure 2). To understand survivorship curves you can use survivorship schedules (*Sx*) to calculate and graph **standardized survivorship** (l_x), **age-specific survivorship** (g_x), and **life expectancy** (e_x).

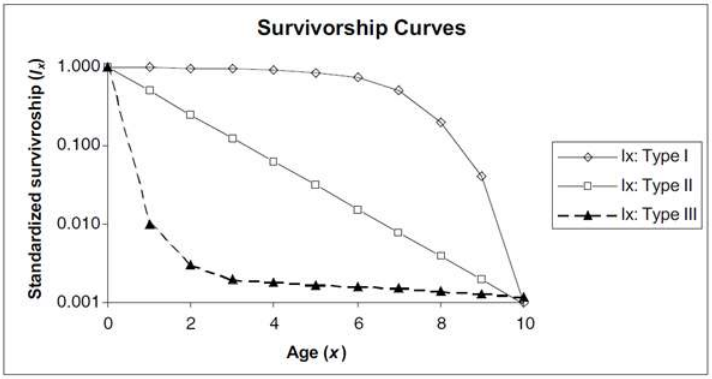


Figure 10.5.3**:** Hypothetical survivorship curves. Note that the *y*-axis has a logarithmic scale. Type 1 organisms have high survivorship throughout life until old age sets in, and then survivorship declines dramatically to 0. Humans are type 1 organisms. Type III organisms, in contrast, have very low survivorship early in life, and few individuals live to old age.

Population Growth or Decline

We frequently want to know whether a population can be expected to grow, shrink, or remain stable, given its current age-specific rates of survival and fecundity. We can determine this by computing the **net reproductive rate** (R_0). To predict long-term changes in population size, we must use this net reproductive rate to estimate the intrinsic rate of increase (r).

Net Reproductive Rate (R_0) We calculate net reproductive rate (R_0) by multiplying the standardized survivorship of each age (l_x) by its fecundity ((b_x)), and summing these products:

$$R_0 = \sum_{x=0}^{k} l_x b_x \tag{10.5.6}$$

The net reproductive rate is the lifetime reproductive potential of the average female, adjusted for survival. Assuming survival and fertility schedules remain constant over time, if $R_0 > 1$, then the population will grow exponentially. If $R_0 < 1$, the population will shrink exponentially, and if $R_0 = 1$, the population size will not change over time. You may be tempted to conclude the $R_0 = r$, the intrinsic rate of increase of the exponential model. However, this is not quite correct, because r measures population change in absolute units of time (e.g., years) whereas R_0 measures population change in terms of generation time. To convert R_0 into r, we must first calculate generation time G, and then adjust R_0.

Generation Time. Generation time is calculated as

$$G = \frac{\sum_{x=0}^{k} l_x b_x x}{\sum_{x=0}^{k} l_x b_x} \tag{10.5.7}$$

For organisms that live only one year, the numerator and denominator will be equal, and generation time will equal to one year. For all longer-lived organisms, generation time will be greater than one year, but exactly how much greater will depend on the survival and fertility schedules. A long-lived species that reproduces at an early age may have a shorter generation time than a shorter-lived one that delays reproduction.

Intrinsic Rate of Increase. We can use our knowledge of exponential population growth and our value of R_0 to estimate the intrinsic rate of increase (r) (Gotelli 2001). The size of an exponentially growing population at some arbitrary time t is $N_t = N_0 e^{rt}$, where e is the base of the natural logarithms and r is the intrinsic rate of increase. If we consider the growth of such a population from time zero through one generation time, G, it is

$$N_G = N_0 e^r G$$

Dividing both sides by N_0 gives us

$$\frac{N_G}{N_0} = e^r G$$

We can think of N_G/N_0 as roughly equivalent to R_0; both are estimates of the rate of population growth over the period of one generation.

Substituting R_0 into the equation gives us

$$R_0 \approx e^r G$$

Taking the natural logarithm of both sides gives us

$$ln(R_0) \approx rG$$

and dividing through by G gives us an estimate of r:

$$r \approx \frac{ln(R_0)}{G}$$

Finally, we can use our estimate of *r* (uncorrected or corrected) to predict the size of the population in the future. This kind of analysis is done for human populations to predict the effects of changes in medical care and birth control programs. If we assume that all age groups are roughly equivalent in size, a similar analysis can be done for endangered species to determine what intervention may be most effective in promoting population growth. The same analysis can be applied to pest species to determine what intervention may be most effective in reducing population size.

Reproductive Value

The idea that different individuals have different "value" in terms of their contribution to future generations is called their *reproductive value* (Fisher 1930). As Caswell (2001) states, "The amount of future reproduction, the probability of surviving to realize it, and the time required for the offspring to be produced all enter into the **reproductive value** of an age-class."

The reproductive value of an individual of age x is designated at V_x, and is the number of offspring that an individual is expected to produce over its remaining life span (after adjusting for the growth rate of the population). Biologists are often interested in knowing the "value" of the different individuals from a practical standpoint because knowing something about the reproductive value can suggest which individuals should be harvested, killed, transplanted, etc. from a conservation or management perspective.

The reproductive value of different ages is strongly tied to an organism's life history. Typically, reproductive value is low at birth, increases to a peak near the age of first reproduction, and then declines (Caswell 2001).

? Life History Table Practice 10.5.1

x	n_x	d_x	q_x	S_x
age	individuals alive at start of age x	age-specific mortality	age-specific mortality rate	age-specific survival rate
---	---	---	$\frac{d_x}{n_x}$ (10.5.8)	$\frac{n_{x+1}}{n_x}$ (10.5.9)
0	125	?	?	?
1	58	?	?	?
2	32	?	?	?
3	16	?	?	?
4	4	?	?	?
5	0	?	?	?

Answer

x	n_x	d_x	q_x	S_x
age	individuals alive at start of age x	age-specific mortality	age-specific mortality rate	age-specific survival rate
---	---	$n_x - n_{x+1}$	$\frac{d_x}{n_x}$ (10.5.10)	$\frac{n_{x+1}}{n_x}$ (10.5.11)
0	125	67	0.54	0.46
1	58	26	0.45	0.55
2	32	16	0.5	0.5
3	16	12	0.75	0.25
4	4	4	1.00	0
5	0	---	---	---

? Life History Table Practice 10.5.2

x	n_x	l_x	L_x	T_x	E_x	b_x
age	individuals alive at start	proportion surviving at start of age x	# surviving	years left to live	life expectancy	average # of female offspring per female
---	---	$\frac{n_x}{n_0}$ (10.5.12)	$\frac{n_x + n_{x+1}}{2}$ (10.5.13)	$\sum_{n=1}^{\infty}(L_x)$ (10.5.14)	$\frac{T_x}{n_x}$ (10.5.15)	---
0	125	?	?	?	?	0
1	58	?	?	?	?	2
2	32	?	?	?	?	3
3	16	?	?	?	?	2
4	4	?	?	?	?	0
5	0	?	?	?	?	0

Answer

x	n_x	l_x	L_x	T_x	E_x	b_x
age	individuals alive at start	proportion surviving at start of age x	# surviving	years left to live	life expectancy	average # of female offspring per female
---	---	$\frac{n_x}{n_0}$ (10.5.16)	$\frac{n_x + n_{x+1}}{2}$ (10.5.17)	$\sum_{n=1}^{\infty}(L_x)$ (10.5.18)	$\frac{T_x}{n_x}$ (10.5.19)	---
0	125	1.00	91.5	172.5	1.38	0
1	58	0.46	45	81	1.40	2
2	32	0.25	24	36	1.13	3
3	16	0.13	10	12	0.75	2
4	4	0.03	2	2	0.5	0
5	0	0	0	0	0	0

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CHAPTER OVERVIEW

Chapter 11: Behavioral Ecology

Learning Objectives

- Explain Tinbergen's levels of analysis and be able to formulate questions that would be addressed at each level of analysis.
- Use concepts from optimal foraging models to explain foraging behavior, and compare and contrast solitary versus group foraging.
- Explain the costs and benefits of migration, and describe how these movements are studied by ecologists.
- Describe the variety forms and functions of animal communication.
- Explain direct, indirect, and inclusive fitness, and use Hamilton's rule to assess when kin selection could be acting in a population.



11.1: Proximate and Ultimate Causes of Behavior
11.1.1: Scientist Spotlight - Ernest Everett Just
11.2: Foraging Ecology
11.3: Movement Ecology
11.4: Animal Communication
11.5: How Does Social Behavior Evolve?
11.6: How Do Social Systems Evolve

Summary

Behavioral ecology is the study of the evolutionary basis for animal behavior due to ecological pressures. Behavioral ecology seeks to address questions associated with the proximate causes, ontogeny, survival value, and phylogeny of a behavior. The field of behavioral ecology includes a variety of disciplines, including the study of how organisms find food, how they move about the environment, and how they communicate with each other. This field is also interested in studying the evolution of social behaviors and social systems.

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11.1: Proximate and Ultimate Causes of Behavior

Behavioral ecology

Behavioral ecology is the study of the evolutionary basis for animal behavior due to ecological pressures. Behavioral ecology emerged after Niko Tinbergen outlined four questions to address when studying animal behaviors: What are the proximate causes, ontogeny, survival value, and phylogeny of a behavior?

In biology, **adaptation** is defined a heritable behavioral, morphological, or physiological trait that has evolved through the process of natural selection, and maintains or increases the fitness of an organism under a given set of environmental conditions. Adaptive traits are those that produce more copies of the individual's genes in future generations. Maladaptive traits are those that leave fewer. For example, if a bird that can call more loudly attracts more mates, then a loud call is an adaptive trait for that population because a louder bird mates more frequently than less loud birds—thus sending more "loud-calling" genes into future generations. Conversely, loud calling birds may attract the attention of predators more often, decreasing their presence in the gene pool.

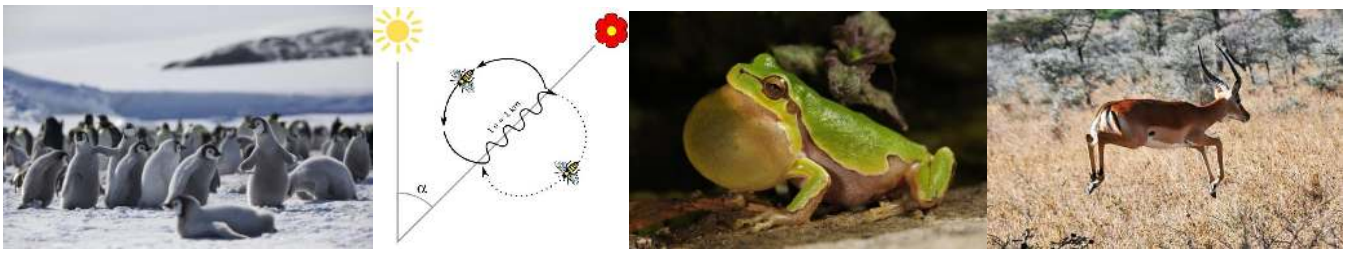


Figure 11.1.1**:** The study of behavioral ecology focuses on the ways organisms behaviorally interact with their physical and social environment. Here we see penguins huddling in the Antarctic (Ian Duffy), the bee waggle dance communicating information (Emmanuel Boutet), a frog with inflated vocal sac (Benny Trapp), and a stotting gazelle (Rick Wilhelmsen).

The study of behavior and Tinbergen's four questions

Tinbergen's four questions, named after Nikolaas Tinbergen, are complementary categories of explanations for animal behaviour. These are also commonly referred to as levels of analysis.[1] It suggests that an integrative understanding of behaviour must include: **ultimate (evolutionary) explanations**, in particular the behaviour (1) **adaptive function** and (2) **phylogenetic** history; and the **proximate explanations**, in particular the (3) underlying **physiological mechanisms** and (4) **ontogenetic/developmental history**.[2]

When asked about the purpose of sight in humans and animals, even elementary-school children can answer that animals have vision to help them find food and avoid danger (function/adaptation). Biologists have three additional explanations: sight is caused by a particular series of evolutionary steps (phylogeny), the mechanics of the eye (mechanism/causation), and even the process of an individual's development (ontogeny).

Table of categories

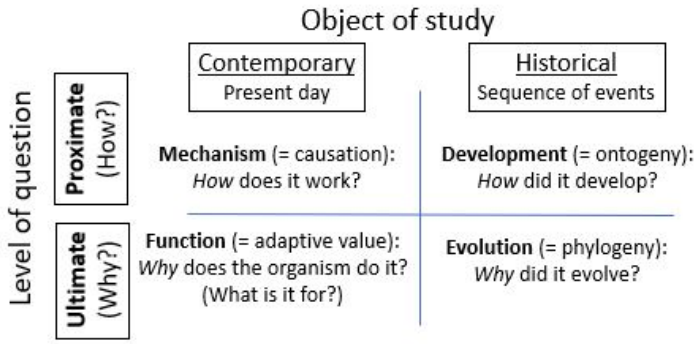


Figure 11.1.2**:** Summary of Tinbergen's four questions (Dan Wetzel).

Evolutionary (ultimate) explanations

1. Function (adaptation)

Darwin's theory of evolution by natural selection is the only scientific explanation for why an animal's behavior is usually well adapted for survival and reproduction in its environment. However, claiming that a particular mechanism is well suited to the present environment is different from claiming that this mechanism was selected for in the past due to its history of being adaptive.[4] The literature conceptualizes the relationship between function and evolution in two ways. On the one hand, function and evolution are often presented as separate and distinct explanations of behaviour.[5]

On the other hand, the common definition of adaptation, a central concept in evolution, is a trait that was functional to the reproductive success of the organism and that is thus now present due to being selected for; that is, function and evolution are inseparable. However a trait can have a current function that is adaptive without being an adaptation in this sense, if for instance the environment has changed. Imagine an environment in which having a small body suddenly conferred benefit on an organism when previously body size had had no effect on survival.[4]

A small body's function in the environment would then be adaptive, but it wouldn't become an adaptation until enough generations had passed in which small bodies were advantageous to reproduction for small bodies to be selected for. Given this, it is best to understand that presently functional traits might not all have been produced by natural selection.[4] The term "function" is preferable to "adaptation", because adaptation is often construed as implying that it was selected for due to past function.

2. Phylogeny (evolution)

Evolution captures both the history of an organism via its phylogeny, and the history of natural selection working on function to produce adaptations.[7] There are several reasons why natural selection may fail to achieve optimal design. One entails random processes such as mutation and environmental events acting on small populations. Another entails the constraints resulting from early evolutionary development. Each organism harbors traits, both anatomical and behavioral, of previous phylogenetic stages, since many traits are retained as populations evolve.

Reconstructing the phylogeny of a species often makes it possible to understand the "uniqueness" of recent characteristics: Earlier phylogenetic stages and (pre-) conditions which persist often also determine the form of more modern characteristics. For instance, the vertebrate eye (including the human eye) has a blind spot, whereas octopus eyes do not. In those two lineages, the eye was originally constructed one way or the other. Once the vertebrate eye was constructed, there were no intermediate forms that were both adaptive and would have enabled it to evolve without a blind spot.

Proximate explanations

3. Mechanism (causation)

In examining living organisms, biologists are confronted with diverse levels of complexity (e.g. chemical, physiological, psychological, social). They therefore investigate causal and functional relations within and between these levels. A biochemist

might examine, for instance, the influence of social and ecological conditions on the release of certain neurotransmitters and hormones, and the effects of such releases on behaviour, e.g. stress during birth has a tocolytic (contraction-suppressing) effect.

Some prominent classes of causal mechanisms include:

- The brain: Broca's area, a small section of the human brain, has a critical role in linguistic capability.
- Hormones: chemicals used to communicate among cells of an individual organism. Testosterone, for instance, stimulates aggressive behaviour in a number of species.
- Pheromones: chemicals used to communicate among members of the same species. Some species (e.g., dogs and some moths) use pheromones to attract mates.

4. Ontogeny

Ontogeny is the process of development of an individual organism from the zygote through the embryo to the adult form.

In the latter half of the twentieth century, social scientists debated whether human behaviour was the product of nature (genes) or nurture (environment in the developmental period, including culture). Many forms of developmental learning have a critical period, for instance, for imprinting among geese and language acquisition among humans. In such cases, genes determine the timing of the environmental impact.

Causal relationships 11.1.1

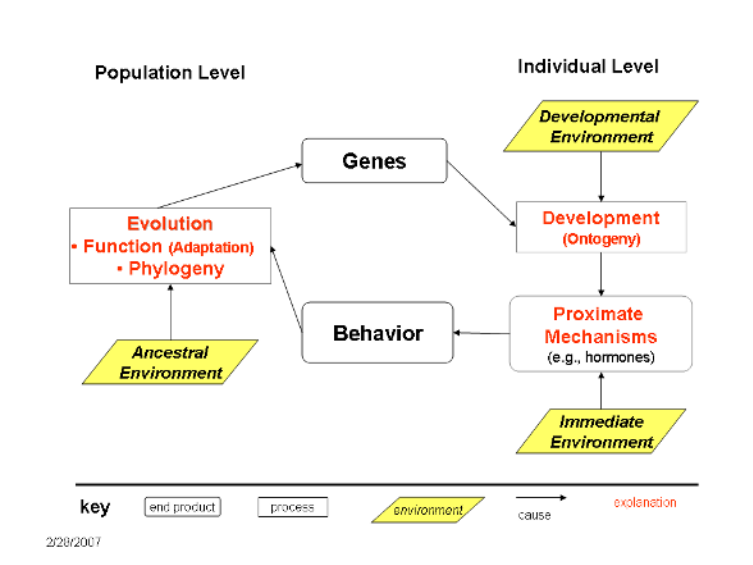


Figure 11.1.3**:** Diagrammatic explanation of behavioral ecology: the interaction between an organisms behavior, its genes, the environment, and evolutionary forces (W. Pete Welch; public domain); Adopted from Tinbergen (1963).

The figure shows the causal relationships among the categories of explanations. The left-hand side represents the evolutionary explanations at the species level; the right-hand side represents the proximate explanations at the individual level. In the middle are those processes' end products—genes (i.e., genome) and behaviour, both of which can be analyzed at both levels.

Evolution, which is determined by both function and phylogeny, results in the genes of a population. The genes of an individual interact with its developmental environment, resulting in mechanisms, such as a nervous system. A mechanism (which is also an end-product in its own right) interacts with the individual's immediate environment, resulting in its behaviour.

Here we return to the population level. Over many generations, the success of the species' behaviour in its ancestral environment—or more technically, the environment of evolutionary adaptedness may result in evolution as measured by a change in its genes.

In sum, there are two processes—one at the population level and one at the individual level—which are influenced by environments in three time periods.

Video



Examples

Let's look at a couple of examples of explaining a trait or behavior using Tinbergen's four questions:

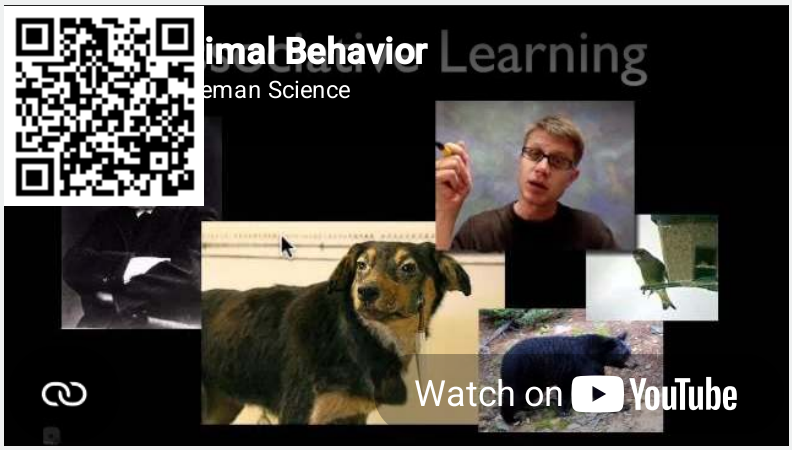
Visual perception

- Function: to find food and avoid danger.
- Phylogeny: the vertebrate eye initially developed with a blind spot, but the lack of adaptive intermediate forms prevented the loss of the blind spot.
- Causation: the lens of the eye focuses light on the retina.
- Development: neurons need the stimulation of light to wire the eye to the brain (Moore, 2001:98–99).

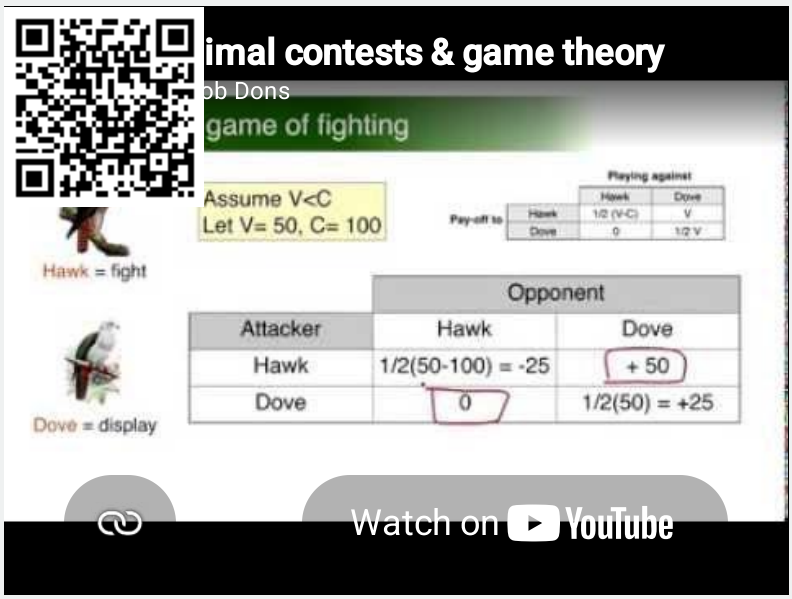
Sleep (Bode & Kuula, 2021):[10]

- Function: energy restoration, metabolic regulation, thermoregulation, boosting immune system, detoxification, brain maturation, circuit reorganization, synaptic optimization, avoiding danger.
- Phylogeny: sleep exists in invertebrates, lower vertebrates, and higher vertebrates. NREM and REM sleep exist in eutheria, marsupialiformes, and also evolved in birds.
- Mechanisms: mechanisms regulate wakefulness, sleep onset, and sleep. Specific mechanisms involve neurotransmitters, genes, neural structures, and the circadian rhythm.
- Ontogeny: sleep manifests differently in babies, infants, children, adolescents, adults, and older adults. Differences include the stages of sleep, sleep duration, and sex differences.

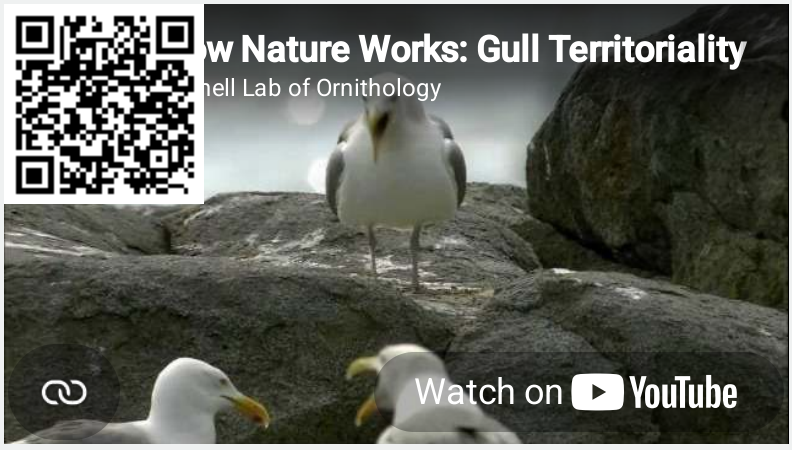
Video



Video



Video



Contributors and Attributions

Modified by Dan Wetzel (University of Pittsburgh) from the following sources:

- Wikipedia, Behavioral ecology
- Wikipedia, Tinbergen's four questions.

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4. Nikolaas Tinbergen
5. Nikolaas Tinbergen, ethology, Cartwright 2000:10; Buss 2004:12)
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7. "Phylogeny" often emphasizes the evolutionary genealogical relationships among species (Alcock 2001:492; Mayr, 2001:289) as distinct from the categories of explanations. Although the categories are more relevant in a conceptual discussion, the traditional term is retained here.
8. "Biased learning" is not necessarily limited to the developmental period.
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11.1.1: Scientist Spotlight - Ernest Everett Just

For those who enjoy them sunny side up, scrambled, or hard boiled, the word “egg” may bring chickens to mind. However, eggs don’t always take the form of smooth, oval-shaped objects that constitute your breakfast, nor do they only come from birds. Scientifically speaking, an “egg” is a gamete, or a sex cell, central to the process of sexual reproduction. This means that eggs are common to all sexually reproducing organisms, even the ones that don’t lay the eggs we’re familiar with.

One type of reproduction, called sexual reproduction, occurs *when a sperm cell fertilizes an egg cell*. The fertilized egg cell is called a “zygote”. When two organisms are involved, the zygote contains genetic material from two different parents. However, sexual reproduction can also occur when one hermaphroditic organism (possessing male and female gametes) self-fertilizes. No matter the number of contributors, the defining mechanism of sexual reproduction is *when a sperm cell fertilizes an egg cell*. This process occurs on a microscopic level, so how do we know what fertilization looks like? One answer to this broad question was unearthed by embryologist Ernest Everett Just. Just was born in Charleston, South Carolina in 1883, and his father died 4 years later (Selassie 2007). He went on to graduate from Dartmouth College, teach English and biology at Howard University, and earn a PhD in zoology at the University of Chicago (Byrnes and Newman 2014). Prior to his time in Chicago, Just conducted research at the Woods Hole Biological Marine Laboratory, where his work with marine invertebrates revealed that the ectoplasm (egg surface) significantly influences the fertilization and development of eggs (Just 1919, 1922; Wellner 2010).

Throughout his career, Just authored more than seventy papers and two books. Despite his major contributions to our understanding of fertilization and evolutionary developmental biology, his work was “...largely forgotten and invisible to the world of biology” (Byrnes and Newman 2014). As an African American man in the early 20th century, Just belonged to a historically marginalized group of people, and he is only now receiving recognition for his pioneering work.



Figure 11.1.1.1**:** "Ernest Everett Just" is available in the public domain.

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Scientist Spotlight Inspiration from the Scientist Spotlights Initiative

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11.2: Foraging Ecology

Foraging



Grizzly bear (*Ursus arctos horribilis*) mother and cubs foraging in Denali National Park, Alaska.

Foraging is searching for wild food resources. It affects an animal's fitness because it plays an important role in an animal's ability to survive and reproduce.[1] Foraging theory is a branch of behavioral ecology that studies the foraging behavior of animals in response to the environment where the animal lives.

Behavioral ecologists use economic models to understand foraging; many of these models are a type of optimal model. Thus foraging theory is discussed in terms of optimizing a payoff from a foraging decision. The payoff for many of these models is the amount of energy an animal receives per unit time, more specifically, the highest ratio of energetic gain to cost while foraging.[2] Foraging theory predicts that the decisions that maximize energy per unit time and thus deliver the highest payoff will be selected for and persist. Key words used to describe foraging behavior include *resources*, the elements necessary for survival and reproduction which have a limited supply, *predator*, any organism that consumes others, *prey*, an organism that is eaten in part or whole by another,[1] and *patches*, concentrations of resources.

Behavioral ecologists first tackled this topic in the 1960s and 1970s. Their goal was to quantify and formalize a set of models to test their null hypothesis that animals forage randomly. Important contributions to foraging theory have been made by:

- Eric Charnov, who developed the marginal value theorem to predict the behavior of foragers using patches;
- Sir John Krebs, with work on the optimal diet model in relation to tits and chickadees;
- John Goss-Custard, who first tested the optimal diet model against behavior in the field, using redshank, and then proceeded to an extensive study of foraging in the common pied oystercatcher

Factors influencing foraging behavior



A troop of olive baboons (*Papio anubis*) foraging in Laikipia, Kenya. Young primates learn from elders in their group about proper foraging.

Several factors affect an animal's ability to forage and acquire profitable resources.

Learning

Learning is defined as an adaptive change or modification of a behavior based on a previous experience.[3] Since an animal's environment is constantly changing, the ability to adjust foraging behavior is essential for maximization of fitness. Studies in social insects have shown that there is a significant correlation between learning and foraging performance.[3]

In nonhuman primates, young individuals learn foraging behavior from their peers and elders by watching other group members forage and by copying their behavior.[4] Observing and learning from other members of the group ensure that the younger members of the group learn what is safe to eat and become proficient foragers.

One measure of learning is 'foraging innovation'—an animal consuming new food, or using a new foraging technique in response to their dynamic living environment.[5] Foraging innovation is considered learning because it involves behavioral plasticity on the

animal's part. The animal recognizes the need to come up with a new foraging strategy and introduce something it has never used before to maximize his or her fitness (survival). Forebrain size has been associated with learning behavior. Animals with larger brain sizes are expected to learn better.[5] A higher ability to innovate has been linked to larger forebrain sizes in North American and British Isle birds according to Lefebvre et al. (1997).[6] In this study, bird orders that contained individuals with larger forebrain sizes displayed a higher amount of foraging innovation. Examples of innovations recorded in birds include following tractors and eating frogs or other insects killed by it and using swaying trees to catch their prey.[5]

Another measure of learning is spatio-temporal learning (also called time-place learning), which refers to an individual's ability to associate the time of an event with the place of that event.[7] This type of learning has been documented in the foraging behaviors of individuals of the stingless bee species *Trigona fulviventris*.[7] Studies showed that *T. fulviventris* individuals learned the locations and times of feeding events, and arrived to those locations up to thirty minutes before the feeding event in anticipation of the food reward.[7]

Genetics



A European honey bee extracts nectar. According to Hunt (2007), two genes have been associated with the sugar concentration of the nectar honey bees collect.

Foraging behavior can also be influenced by genetics. The genes associated with foraging behavior have been widely studied in honeybees with reference to the following; onset of foraging behavior, task division between foragers and workers, and bias in foraging for either pollen or nectar.[5][8] Honey bee foraging activity occurs both inside and outside the hive for either pollen or nectar. Similar behavior is seen in many social wasps, such as the species *Apoica flavissima*. Studies using quantitative trait loci (QTL) mapping have associated the following loci with the matched functions; Pln-1 and Pln-4 with onset of foraging age, Pln-1 and 2 with the size of the pollen loads collected by workers, and Pln-2 and pln-3 were shown to influence the sugar concentration of the nectar collected.[8]

Predators and parasites

The presence of predators while a (prey) animal is foraging affects its behaviour. In general, foragers balance the risk of predation with their needs, thus deviating from the foraging behaviour that would be expected in the absence of predators.[9]

Similarly, parasitism can affect the way in which animals forage. Parasitism can affect foraging at several levels. Animals might simply avoid food items that increase their risk of being parasitized, as when the prey items are intermediate hosts of parasites. Animals might also avoid areas that would expose them to a high risk of parasitism. Finally, animals might effectively self-medicate, either prophylactically or therapeutically.

Types of foraging

Foraging can be categorized into two main types. The first is solitary foraging, when animals forage by themselves. The second is group foraging.

Solitary foraging

Solitary foraging includes the variety of foraging in which animals find, capture and consume their prey alone. Individuals can manually exploit patches or they can use tools to exploit their prey. For example, Bolas spiders attack their prey by luring them with a scent identical to the female moth's sex pheromones.[11] Animals may choose to forage on their own when the resources are abundant, which can occur when the habitat is rich or when the number of conspecifics foraging are few. In these cases there may be no need for group foraging.[12] In addition, foraging alone can result in less interaction with other foragers, which can decrease the amount of competition and dominance interactions an animal deals with. It will also ensure that a solitary forager is less conspicuous to predators.[13] Solitary foraging strategies characterize many of the phocids (the true seals) such as the elephant and

harbor seals. An example of an exclusive solitary forager is the South American species of the harvester ant, *Pogonomyrmex vermiculatus*.[14]

Solitary foraging and optimal foraging theory

The theory scientists use to understand solitary foraging is called optimal foraging theory (described in detail below). This theory argues that because of the key importance of successful foraging to an individual's survival, it should be possible to predict foraging behavior by using decision theory to determine the behavior that an "optimal forager" would exhibit. Such a forager has perfect knowledge of what to do to maximize usable food intake. While the behavior of real animals inevitably departs from that of the optimal forager, optimal foraging theory has proved very useful in developing hypotheses for describing real foraging behavior. Departures from optimality often help to identify constraints either in the animal's behavioral or cognitive repertoire, or in the environment, that had not previously been suspected. With those constraints identified, foraging behavior often does approach the optimal pattern even if it is not identical to it. In other words, we know from optimal foraging theory that animals are not foraging randomly even if their behavior doesn't perfectly match what is predicted by OFT.

Group foraging

Group foraging is when animals find, capture and consume prey in the presence of other individuals. In other words, it is foraging when success depends not only on your own foraging behaviors but the behaviors of others as well.[20] An important note here is that group foraging can emerge in two types of situations. The first situation is frequently thought of and occurs when foraging in a group is beneficial and brings greater rewards known as an aggregation economy.[1] The second situation occurs when a group of animals forage together but it may not be in an animal's best interest to do so known as a dispersion economy. Think of a cardinal at a bird feeder for the dispersion economy. We might see a group of birds foraging at that bird feeder but it is not in the best interest of the cardinal for any of the other birds to be there too. The amount of food the cardinal can get from that bird feeder depends on how much it can take from the bird feeder but also depends on how much the other birds take as well.



A male northern cardinal at a bird feeder. Birds feeding at a bird feeder is an example of a dispersion economy. This is when it may not be in an animal's best interest to forage in a group.

In red harvester ants, the foraging process is divided between three different types of workers: nest patrollers, trail patrollers, and foragers. These workers can utilize many different methods of communicating while foraging in a group, such as guiding flights, scent paths, and "jostling runs", as seen in the eusocial bee *Melipona scutellaris*.[21]

Chimpanzees in the Taï Forest in Côte d'Ivoire also engage in foraging for meats when they can, which is achieved through group foraging. Positive correlation has been observed between the success of the hunt and the size of the foraging group. The chimps have also been observed implying rules with their foraging, where there is a benefit to becoming involved through allowing successful hunters first access to their kills.[22][23][24]

Cost and benefits of group foraging



Female lions make foraging decisions and more specifically decisions about hunting group size with protection of their cubs and territory defense in mind.[25]

As already mentioned, group foraging brings both costs and benefits to the members of that group. Some of the benefits of group foraging include being able to capture larger prey,[25] being able to create aggregations of prey,[26] being able to capture prey that are difficult or dangerous and most importantly reduction of predation threat.[20] With regard to costs, however, group foraging results in competition for available resources by other group members. Competition for resources can be characterized by either scramble competition whereby each individual strives to get a portion of the shared resource, or by interference competition whereby the presence of competitors prevents a forager's accessibility to resources.[1] Group foraging can thus reduce an animal's foraging payoff.[20]

Group foraging may be influenced by the size of a group. In some species like lions and wild dogs, foraging success increases with an increase in group size then declines once the optimal size is exceeded. A myriad number of factors affect the group sizes in different species. For example, lionesses (female lions) do not make decisions about foraging in a vacuum. They make decisions that reflect a balance between obtaining food, defending their territory and protecting their young. In fact, we see that lion foraging behavior does not maximize their energy gain. They are not behaving optimally with respect to foraging because they have to defend their territory and protect young so they hunt in small groups to reduce the risk of being caught alone.[25] Another factor that may influence group size is the cost of hunting. To understand the behavior of wild dogs and the average group size we must incorporate the distance the dogs run.[27]

Group foraging and the ideal free distribution

The theory scientists use to understand group foraging is called the Ideal free distribution. This is the null model for thinking about what would draw animals into groups to forage and how they would behave in the process. This model predicts that animals will make an instantaneous decision about where to forage based on the quality (prey availability) of the patches available at that time and will choose the most profitable patch, the one that maximizes their energy intake. This quality depends on the starting quality of the patch and the number of predators already there consuming the prey.

Video



BIO 270 Material: Optimal foraging theory



Worker bees forage nectar not only for themselves, but for their whole hive community. Optimal foraging theory predicts that this bee will forage in a way that will maximize its hive's net yield of energy.

Optimal foraging theory (**OFT**) is a behavioral ecology model that helps predict how an animal behaves when searching for food. Although obtaining food provides the animal with energy, searching for and capturing the food require both energy and time. To maximize fitness, an animal adopts a foraging strategy that provides the most benefit (energy) for the lowest cost, maximizing the net energy gained. OFT helps predict the best strategy that an animal can use to achieve this goal.

OFT is an ecological application of the optimality model. This theory assumes that the most economically advantageous foraging pattern will be selected for in a species through natural selection.[29] When using OFT to model foraging behavior, organisms are said to be maximizing a variable known as the **currency**, such as the most food per unit time. In addition, the **constraints** of the environment are other variables that must be considered. Constraints are defined as factors that can limit the forager's ability to maximize the currency. The **optimal decision rule**, or the organism's best foraging strategy, is defined as the decision that maximizes the currency under the constraints of the environment. Identifying the optimal decision rule is the primary goal of the OFT.[30]

Building an optimal foraging model

An optimal foraging model generates quantitative predictions of how animals maximize their fitness while they forage. The model building process involves identifying the currency, constraints, and appropriate decision rule for the forager.[30][31]

Currency is defined as the unit that is optimized by the animal. It is also a hypothesis of the costs and benefits that are imposed on that animal.[32] For example, a certain forager gains energy from food, but incurs the cost of searching for the food: the time and energy spent searching could have been used instead on other endeavors, such as finding mates or protecting young. It would be in the animal's best interest to maximize its benefits at the lowest cost. Thus, the currency in this situation could be defined as net energy gain per unit time.[30] However, for a different forager, the time it takes to digest the food after eating could be a more significant cost than the time and energy spent looking for food. In this case, the currency could be defined as net energy gain per digestive turnover time instead of net energy gain per unit time.[33] Furthermore, benefits and costs can depend on a forager's community. For example, a forager living in a hive would most likely forage in a manner that would maximize efficiency for its colony rather than itself.[32] By identifying the currency, one can construct a hypothesis about which benefits and costs are important to the forager in question.

Constraints are hypotheses about the limitations that are placed on an animal.[32] These limitations can be due to features of the environment or the physiology of the animal and could limit their foraging efficiency. The time that it takes for the forager to travel from the nesting site to the foraging site is an example of a constraint. The maximum number of food items a forager is able to carry back to its nesting site is another example of a constraint. There could also be cognitive constraints on animals, such as limits to learning and memory.[30] The more constraints that one is able to identify in a given system, the more predictive power the model will have.[32]

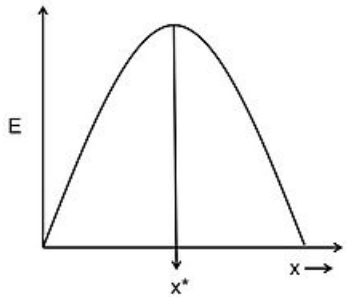


Figure 1. Energy gain per cost (E) for adopting foraging strategy x. Adapted from Parker & Smith.[34]

Given the hypotheses about the currency and the constraints, the **optimal decision rule** is the model's prediction of what the animal's best foraging strategy should be.[30] Possible examples of optimal decision rules could be the optimal number of food items that an animal should carry back to its nesting site or the optimal size of a food item that an animal should feed on. Figure 1, shows an example of how an optimal decision rule could be determined from a graphical model.[34] The curve represents the energy gain per cost (E) for adopting foraging strategy x. Energy gain per cost is the currency being optimized. The constraints of the system determine the shape of this curve. The optimal decision rule (x*) is the strategy for which the currency, energy gain per costs, is the greatest. Optimal foraging models can look very different and become very complex, depending on the nature of the currency and the number of constraints considered. However, the general principles of currency, constraints, and optimal decision rule remain the same for all models.

To test a model, one can compare the predicted strategy to the animal's actual foraging behavior. If the model fits the observed data well, then the hypotheses about the currency and constraints are supported. If the model doesn't fit the data well, then it is possible that either the currency or a particular constraint has been incorrectly identified.[32]

Different feeding systems and classes of predators

Optimal foraging theory is widely applicable to feeding systems throughout the animal kingdom. Under the OFT, *any* organism of interest can be viewed as a predator that forages prey. There are different classes of predators that organisms fall into and each class has distinct foraging and predation strategies.

- **True predators** attack large numbers of prey throughout their life. They kill their prey either immediately or shortly after the attack. They may eat all or only part of their prey. True predators include tigers, lions, whales, sharks, seed-eating birds, ants.[35]
- **Grazers** eat only a portion of their prey. They harm the prey, but rarely kill it. Grazers include antelope, cattle, and mosquitoes.
- **Parasites**, like grazers, eat only a part of their prey (host), but rarely the entire organism. They spend all or large portions of their life cycle living in/on a single host. This intimate relationship is typical of tapeworms, liver flukes, and plant parasites, such as the potato blight.
- **Parasitoids** are mainly typical of wasps (order *Hymenoptera*), and some flies (order *Diptera*). Eggs are laid inside the larvae of other arthropods which hatch and consume the host from the inside, killing it. This unusual predator–host relationship is typical of about 10% of all insects.[36] Many viruses that attack single-celled organisms (such as bacteriophages) are also parasitoids; they reproduce inside a single host that is inevitably killed by the association.

The optimization of these different foraging and predation strategies can be explained by the optimal foraging theory. In each case, there are costs, benefits, and limitations that ultimately determine the optimal decision rule that the predator should follow.

The optimal diet model

One classical version of the optimal foraging theory is the **optimal diet model**, which is also known as the prey choice model or the contingency model. In this model, the predator encounters different prey items and decides whether to eat what it has or search for a more profitable prey item. The model predicts that foragers should ignore low profitability prey items when more profitable items are present and abundant.[37]

The profitability of a prey item is dependent on several ecological variables. **E** is the amount of energy (calories) that a prey item provides the predator. Handling time (**h**) is the amount of time it takes the predator to handle the food, beginning from the time the predator finds the prey item to the time the prey item is eaten. The profitability of a prey item is then defined as **E/h**. Additionally, search time (**S**) is the amount of time it takes the predator to find a prey item and is dependent on the abundance of the food and the ease of locating it.[30] In this model, the currency is energy intake per unit time and the constraints include the actual values of **E**, **h**, and **S**, as well as the fact that prey items are encountered sequentially.

Model of choice between big and small prey

Using these variables, the optimal diet model can predict how predators choose between two prey types: big **prey1** with energy value **E1** and handling time **h1**, and small **prey2** with energy value **E2** and handling time **h2**. In order to maximize its overall rate of energy gain, a predator must consider the profitability of the two prey types. If it is assumed that big prey1 is more profitable than small prey2, then **E1/h1 > E2/h2**. Thus, if the predator encounters prey1, it should always choose to eat it, because of its higher profitability. It should never bother to go searching for prey2. However, if the animal encounters prey2, it should reject it to look for a more profitable prey1, *unless* the time it would take to find prey1 is too long and costly for it to be worth it. Thus, the animal should eat prey2 only if **E2/h2 > E1/(h1+S1)**, where **S1** is the search time for prey1. Since it is always favorable to choose to eat prey1, the choice to eat prey1 is not dependent on the abundance of prey2. But since the length of **S1** (i.e. how difficult it is to find prey1) is logically dependent on the density of prey1, the choice to eat prey2 *is* dependent on the abundance of prey1.[32]

Generalist and specialist diets

The optimal diet model also predicts that different types of animals should adopt different diets based on variations in search time. This idea is an extension of the model of prey choice that was discussed above. The equation, **E2/h2 > E1/(h1+S1)**, can be rearranged to give: **S1 > [(E1h2)/E2] – h1**. This rearranged form gives the threshold for how long **S1** must be for an animal to choose to eat both prey1 and prey2.[32] Animals that have **S1**'s that reach the threshold are defined as generalists. In nature, generalists include a wide range of prey items in their diet.[38] An example of a generalist is a mouse, which consumes a large variety of seeds, grains, and nuts.[39] In contrast, predators with relatively short **S1**'s are still better off choosing to eat only prey1. These types of animals are defined as specialists and have very exclusive diets in nature.[38] An example of a specialist is the koala, which solely consumes eucalyptus leaves.[40] In general, different animals across the four functional classes of predators exhibit strategies ranging across a continuum between being a generalist and a specialist. Additionally, since the choice to eat prey2 is dependent on the abundance of prey1 (as discussed earlier), if prey1 becomes so scarce that S1 reaches the threshold, then the animal should switch from exclusively eating prey1 to eating both prey1 and prey2.[32] In other words, if the food within a specialist's diet becomes very scarce, a specialist can sometimes switch to being a generalist.

Functional response curves

As previously mentioned, the amount of time it takes to search for a prey item depends on the density of the prey. Functional response curves show the rate of prey capture as a function of food density and can be used in conjunction with the optimal diet theory to predict foraging behavior of predators. There are three different types of functional response curves.[41]

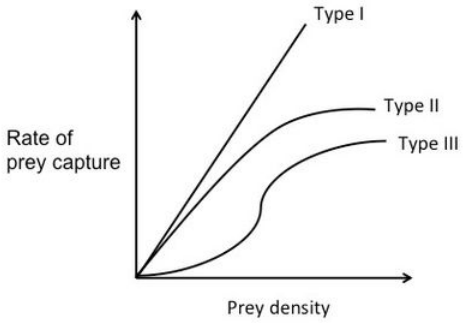


Figure 2. Three types of functional response curves. Adapted from Staddon.[41]

For a **Type I** functional response curve, the rate of prey capture increases linearly with food density. At low prey densities, the search time is long. Since the predator spends most of its time searching, it eats every prey item it finds. As prey density increases,

the predator is able to capture the prey faster and faster. At a certain point, the rate of prey capture is so high, that the predator doesn't have to eat every prey item it encounters. After this point, the predator should choose only the prey items with the highest E/h.[42]

For a **Type II** functional response curve, the rate of prey capture negatively accelerates as it increases with food density.[41] This is because it assumes that the predator is limited by its capacity to process food. In other words, as the food density increases, handling time increases. At the beginning of the curve, rate of prey capture increases nearly linearly with prey density and there is almost no handling time. As prey density increases, the predator spends less and less time searching for prey and more and more time handling the prey. The rate of prey capture increases less and less, until it finally plateaus. The high number of prey basically "swamps" the predator.[42]

A **Type III** functional response curve is a sigmoid curve. The rate of prey capture increases at first with prey density at a positively accelerated rate, but then at high densities changes to the negatively accelerated form, similar to that of the Type II curve.[41] At high prey densities (the top of the curve), each new prey item is caught almost immediately. The predator is able to be choosy and doesn't eat every item it finds. So, assuming that there are two prey types with different profitabilities that are both at high abundance, the predator will choose the item with the higher **E/h**. However, at low prey densities (the bottom of the curve) the rate of prey capture increases faster than linearly. This means that as the predator feeds and the prey type with the higher **E/h** becomes less abundant, the predator will start to switch its preference to the prey type with the lower **E/h**, because that type will be relatively more abundant. This phenomenon is known as prey switching.[41]

Predator–prey interaction

Predator–prey coevolution often makes it unfavorable for a predator to consume certain prey items, since many anti-predator defenses increase handling time.[43] Examples include porcupine quills, the palatability and digestibility of the poison dart frog, crypsis, and other predator avoidance behaviors. In addition, because toxins may be present in many prey types, predators include a lot of variability in their diets to prevent any one toxin from reaching dangerous levels. Thus, it is possible that an approach focusing only on energy intake may not fully explain an animal's foraging behavior in these situations.

The marginal value theorem and optimal foraging

The **marginal value theorem** is a type of optimality model that is often applied to optimal foraging. This theorem is used to describe a situation in which an organism searching for food in a patch must decide when it is economically favorable to leave. While the animal is within a patch, it experiences the law of diminishing returns, where it becomes harder and harder to find prey as time goes on. This may be because the prey is being depleted, the prey begins to take evasive action and becomes harder to catch, or the predator starts crossing its own path more as it searches.[32] This law of diminishing returns can be shown as a curve of energy gain per time spent in a patch (Figure 3). The curve starts off with a steep slope and gradually levels off as prey becomes harder to find. Another important cost to consider is the traveling time between different patches and the nesting site. An animal loses foraging time while it travels and expends energy through its locomotion.[30]

In this model, the currency being optimized is usually net energy gain per unit time. The constraints are the travel time and the shape of the curve of diminishing returns. Graphically, the currency (net energy gain per unit time) is given by the slope of a diagonal line that starts at the beginning of traveling time and intersects the curve of diminishing returns (Figure 3). In order to maximize the currency, one wants the line with the greatest slope that still touches the curve (the tangent line). The place that this line touches the curve provides the optimal decision rule of the amount of time that the animal should spend in a patch before leaving.

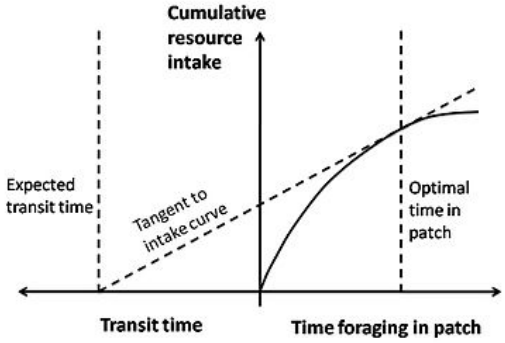


Figure 3. Marginal value theorem shown graphically.

Examples of optimal foraging models in animals

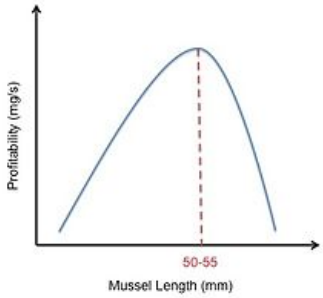


Figure 4. Right-shifted mussel profitability curve. Adapted from Meire & Ervynck.[44]

Optimal foraging of oystercatchers

Oystercatcher mussel feeding provides an example of how the optimal diet model can be utilized. Oystercatchers forage on mussels and crack them open with their bills. The constraints on these birds are the characteristics of the different mussel sizes. While large mussels provide more energy than small mussels, large mussels are harder to crack open due to their thicker shells. This means that while large mussels have a higher energy content (**E**), they also have a longer handling time (**h**). The profitability of any mussel is calculated as **E/h**. The oystercatchers must decide which mussel size will provide enough nutrition to outweigh the cost and energy required to open it.[2] In their study, Meire and Ervynck tried to model this decision by graphing the relative profitabilities of different sized mussels. They came up with a bell-shaped curve, indicating that moderately sized mussels were the most profitable. However, they observed that if an oystercatcher rejected too many small mussels, the time it took to search for the next suitable mussel greatly increased. This observation shifted their bell-curve to the right (Figure 4). However, while this model predicted that oystercatchers should prefer mussels of 50–55 mm, the observed data showed that oystercatchers actually prefer mussels of 30–45 mm. Meire and Ervynk then realized the preference of mussel size did not depend only on the profitability of the prey, but also on the prey density. After this was accounted for, they found a good agreement between the model's prediction and the observed data.[44]

Optimal foraging in starlings

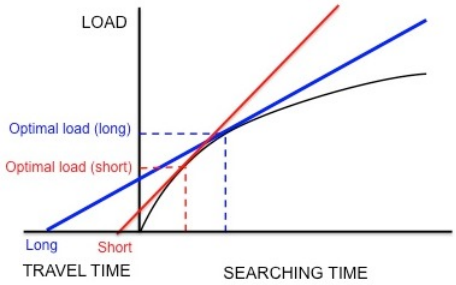
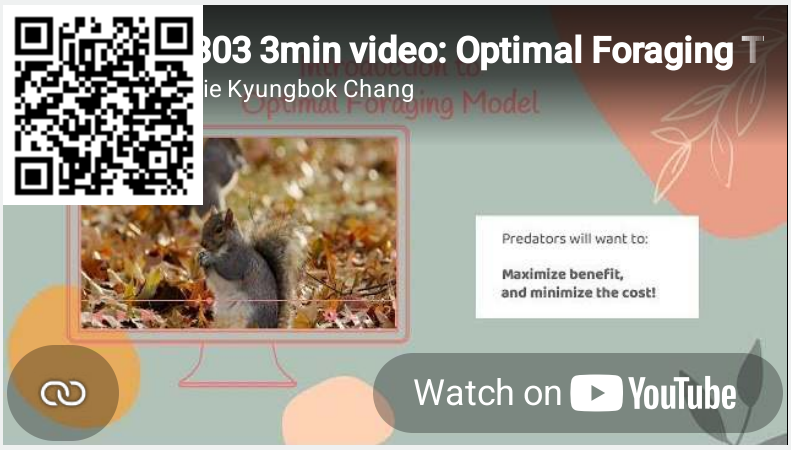


Figure 5. If starlings are maximizing net rate of energy gain, longer traveling time results in larger optimum load. Adapted from Krebs and Davies.[32]

The foraging behavior of the European starling, *Sturnus vulgaris*, provides an example of how marginal value theorem is used to model optimal foraging. Starlings leave their nests and travel to food patches in search for larval leatherjackets to bring back to their young. The starlings must determine the optimal number of prey items to take back in one trip (i.e. the optimal load size). While the starlings forage within a patch, they experience diminishing returns: the starling is able to hold only so many leatherjackets in its bill, so the speed with which the parent picks up larvae decreases with the number of larvae that it already has in its bill. Thus, the constraints are the shape of the curve of diminishing returns and the travel time (the time it takes to make a round trip from the nest to a patch and back). In addition, the currency is hypothesized to be net energy gain per unit time.[32] Using this currency and the constraints, the optimal load can be predicted by drawing a line tangent to the curve of diminishing returns, as discussed previously (Figure 3).

Kacelnik et al. wanted to determine if this species does indeed optimize net energy gain per unit time as hypothesized.[45] They designed an experiment in which the starlings were trained to collect mealworms from an artificial feeder at different distances from the nest. The researchers artificially generated a fixed curve of diminishing returns for the birds by dropping mealworms at successively longer and longer intervals. The birds continued to collect mealworms as they were presented, until they reached an "optimal" load and flew home. As Figure 5 shows, if the starlings were maximizing net energy gain per unit time, a short travel time would predict a small optimal load and a long travel time would predict a larger optimal load. In agreement with these predictions, Kacelnik found that the longer the distance between the nest and the artificial feeder, the larger the load size. In addition, the observed load sizes quantitatively corresponded very closely to the model's predictions. Other models based on different currencies, such as energy gained per energy spent (i.e. energy efficiency), failed to predict the observed load sizes as accurately. Thus, Kacelnik concluded that starlings maximize net energy gain per unit time. This conclusion was not disproved in later experiments.[46][47]

Video



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11.3: Movement Ecology

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Animal Migration

Video



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11.4: Animal Communication

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An Introduction to Animal Communication

Video





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How Does Social Behavior Evolve?

Video



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11.6: How Do Social Systems Evolve

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Cooperation, Conflict, and the Evolution of Complex Animal Societies

Rubenstein, D. & Kealey, J. (2010) Cooperation, Conflict, and the Evolution of Complex Animal Societies. *Nature Education Knowledge* 3(10):78

Chapter summary

Behavioral ecology is the study of the evolutionary basis for animal behavior due to ecological pressures. Behavioral ecology seeks to address questions associated with the proximate causes, ontogeny, survival value, and phylogeny of a behavior. The field of behavioral ecology includes a variety of disciplines, including the study of how organisms find food, how they move about the environment, and how they communicate with each other. This field is also interested in studying the evolution of social behaviors and social systems.

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CHAPTER OVERVIEW

Chapter 12: Sex Strategies

Learning Objectives

- Compare and contrast the costs and benefits of asexual reproduction versus sexual reproduction, and explain hypotheses for the evolution of sexual reproduction.
- Explain the variety of ways in which sexes are determined across plants and animals.
- Describe different types of mating systems in plants and animals.
- Describe the different forms of sexual selection, and explain hypotheses for the evolution of female choice.

12.1: The paradox of sex: sexual versus asexual reproduction
12.2: Sex determination and sex ratios
12.3: Mating systems in sexual animals
12.4: Mating Systems in Plants
12.5: Sexual selection

Summary

The paradox of sexual reproduction is that although it is ubiquitous in multicellular organisms, there are many disadvantages to reproducing sexually when we compare it to asexual reproduction. This chapter explores some of the multitude of hypotheses for why sexual reproduction exists, the variety of ways in which sexes are determined in plants and animals, and some of the variation in mating systems of sexual organisms. This chapter also focuses on sexual selection, a form of natural selection that occurs when traits that improve mating success are favored by selection, even if they cause a decrease in survival.

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12.1: The paradox of sex: sexual versus asexual reproduction

The Paradox of Sex

Sexual Reproduction

Sexual reproduction is a type of reproduction that involves a complex life cycle in which a gamete (such as a sperm or egg cell) with a single set of chromosomes (haploid) combines with another to produce a zygote that develops into an organism composed of cells with two sets of chromosomes (diploid) (Maynard Smith & Szathmáry, 1995). Sexual reproduction is the most common life cycle in multicellular eukaryotes, such as animals, fungi and plants. Sexual reproduction does not occur in prokaryotes (organisms without cell nuclei), but they have processes with similar effects such as bacterial conjugation, transformation and transduction, which may have been precursors to sexual reproduction in early eukaryotes.

In the production of sex cells in eukaryotes, diploid mother cells divide to produce haploid cells known as gametes in a process called meiosis that involves genetic recombination. The homologous chromosomes pair up so that their DNA sequences are aligned with each other, and this is followed by exchange of genetic information between them. Two rounds of cell division then produce four haploid gametes, each with half the number of chromosomes from each parent cell, but with the genetic information in the parental chromosomes recombined. Two haploid gametes combine into one diploid cell known as a zygote in a process called fertilization. The zygote incorporates genetic material from both gametes. Multiple cell divisions, without change of the number of chromosomes, then form a multicellular diploid phase or generation.

The evolution of sexual reproduction is considered paradoxical, because asexually reproducing individuals should be able to outperform sexually reproducing individuals (Otto 2014). This is because every offspring produced by an asexually reproducing individual can produce its own own offspring, while sexually reproducing individuals must produce two sexes: one to fertilize the opposite sex and one to produce/bear offspring. This implies that an asexual population has an intrinsic capacity to grow more rapidly with each generation (Maynard Smith, 1978). This 50% cost is a fitness disadvantage of sexual reproduction (Ridley, 2004). The two-fold cost of sex includes this cost and the fact that any organism can only pass on 50% of its own genes to its offspring. One definite advantage of sexual reproduction is that it impedes the accumulation of genetic mutations (Hussin et al., 2015).

The first fossilized evidence of sexual reproduction in eukaryotes is from the Stenian period, about 1.05 billion years ago (Butterfield, 2000; Gibson, 2018).

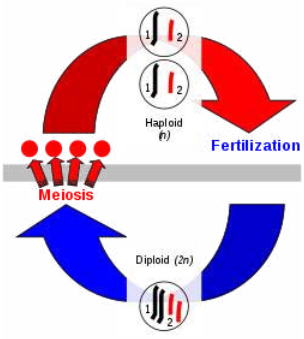


Figure 12.1.1**:** In the first stage of sexual reproduction, "meiosis", the number of chromosomes is reduced from a diploid number (2n) to a haploid number (n). During "fertilization", haploid gametes come together to form a diploid zygote, and the original number of chromosomes is restored.

Asexual Reproduction

Asexual reproduction is a type of reproduction that does not involve the fusion of gametes or change in the number of chromosomes. The offspring that arise by asexual reproduction from either unicellular or multicellular organisms inherit the full set of genes of their single parent. Asexual reproduction is the primary form of reproduction for single-celled organisms such as

archaea and bacteria. Many eukaryotic organisms including plants, animals, and fungi can also reproduce asexually (Engelstädter, 2017). In vertebrates, the most common form of asexual reproduction is parthenogenesis (described below), which is typically used as an alternative to sexual reproduction in times when reproductive opportunities are limited (Dudgeon et al., 2017).

While all prokaryotes reproduce without the formation and fusion of gametes, mechanisms for lateral gene transfer such as conjugation, transformation and transduction can be likened to sexual reproduction in the sense of genetic recombination in meiosis (Narra & Ochman, 2006).

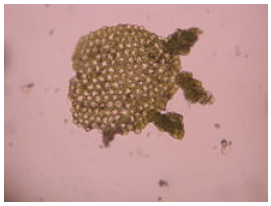


Figure 12.1.2**:** Asexual reproduction in liverworts: a caducous phylloid germinating.

Types of Asexual Reproduction

Fission

Prokaryotes (archaea and bacteria) reproduce asexually through binary fission, in which the parent organism divides in two to produce two genetically identical daughter organisms. Eukaryotes (such as protists and unicellular fungi) may reproduce in a functionally similar manner by mitosis; most of these are also capable of sexual reproduction.

Multiple fission at the cellular level occurs in many protists, e.g. sporozoans and algae. The nucleus of the parent cell divides several times by mitosis, producing several nuclei. The cytoplasm then separates, creating multiple daughter cells (Encyclopædia Britannica, n.d.; Britannica Educational Publishing, 2011; Puranik & Bhate, 2007).

Budding

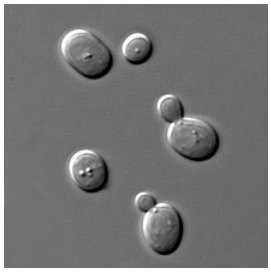


Figure 12.1.3**:** The yeast *Saccharomyces cerevisiae* reproducing by budding.

Some cells divide by budding (for example baker's yeast), resulting in a "mother" and a "daughter" cell that is initially smaller than the parent. Budding is also known on a multicellular level; an animal example is the hydra, which reproduces by budding (Leeuwenhoek, 1703). The buds grow into fully matured individuals which eventually break away from the parent organism.

Internal budding is a process of asexual reproduction, favored by parasites such as *Toxoplasma gondii*. It involves an unusual process in which two (*endodyogeny*) or more (*endopolygeny*) daughter cells are produced inside a mother cell, which is then consumed by the offspring prior to their separation (Smyth, 1994).

Vegetative Propagation

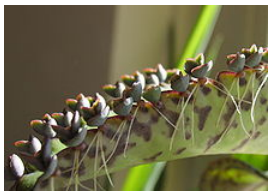


Figure 12.1.4**:** Vegetative plantlets of mother-of-thousands, *Bryophyllum daigremontianum (Kalanchoe daigremontiana).*

Vegetative propagation is a type of asexual reproduction found in plants where new individuals are formed without the production of seeds or spores and thus without syngamy or meiosis (University of California Museum of Paleontology, nd). Examples of vegetative reproduction include the formation of miniaturized plants called plantlets on specialized leaves, for example in kalanchoe (*Bryophyllum daigremontianum*) and many produce new plants from rhizomes or stolon (for example in strawberry). Other plants reproduce by forming bulbs or tubers (for example tulip bulbs and *Dahlia* tubers). Some plants produce adventitious shoots and may form a clonal colony. In these examples, all the individuals are clones, and the clonal population may cover a large area (U.S. Forest Service, 2010).

Spore Formation

Many multicellular organisms form spores during their biological life cycle in a process called *sporogenesis*. Exceptions are animals and some protists, which undergo *meiosis* immediately followed by fertilization. Plants and many algae on the other hand undergo *sporic meiosis* where meiosis leads to the formation of haploid spores rather than gametes. These spores grow into multicellular individuals (called gametophytes in the case of plants) without a fertilization event. These haploid individuals give rise to gametes through mitosis. Meiosis and gamete formation therefore occur in separate generations or "phases" of the life cycle, referred to as alternation of generations. Since sexual reproduction is often more narrowly defined as the fusion of gametes (fertilization), spore formation in plant sporophytes and algae might be considered a form of asexual reproduction (agamogenesis) despite being the result of meiosis and undergoing a reduction in ploidy. However, both events (spore formation and fertilization) are necessary to complete sexual reproduction in the plant life cycle.

Fungi and some algae can also utilize true asexual spore formation, which involves mitosis giving rise to reproductive cells called mitospores that develop into a new organism after dispersal. This method of reproduction is found for example in conidial fungi and the red algae *Polysiphonia*, and involves sporogenesis without meiosis. Thus the chromosome number of the spore cell is the same as that of the parent producing the spores.

Fragmentation



Figure 12.1.5**:** *Linckia guildingi* "comet", a starfish regrowing from a single arm.

Fragmentation is a form of asexual reproduction where a new organism grows from a fragment of the parent. Each fragment develops into a mature, fully grown individual. Fragmentation is seen in many organisms. Animals that reproduce asexually include planarians, many annelid worms including polychaetes and some oligochaetes, turbellarians and sea stars (Ruppert et al., 2004). Many fungi and plants reproduce asexually. Some plants have specialized structures for reproduction via fragmentation, such as *gemmae* in liverworts. Most lichens, which are a symbiotic union of a fungus and photosynthetic algae or cyanobacteria, reproduce through fragmentation to ensure that new individuals contain both symbionts.

Parthenogenesis

Parthenogenesis is a form of agamogenesis in which an unfertilized egg develops into a new individual. It has been documented in over 2,000 species (Sköld et al., 2009). Parthenogenesis occurs in the wild in many invertebrates (e.g. water fleas, rotifers, aphids, stick insects, some ants, bees and parasitic wasps) and vertebrates (mostly reptiles, amphibians, and fish). It has also been documented in domestic birds and in genetically altered lab mice (Neuhof et al., 2016; Ramachandran & McDaniel, 2018). Plants can engage in parthenogenesis as well through a process called apomixis. However this process is considered by many to not be an independent reproduction method, but instead a breakdown of the mechanisms behind sexual reproduction (Ozias-Akins & Conner, 2012). Parthenogenetic organisms can be split into two main categories: facultative and obligate.

The Evolution of Sex

Sexual reproduction is an adaptive feature which is common to almost all multi-cellular organisms (and also some single-cellular organisms) with many being incapable of reproducing asexually. Prior to the advent of sexual reproduction, the adaptation process whereby genes would change from one generation to the next (genetic mutation) happened very slowly and randomly. Sex evolved as an extremely efficient mechanism for producing variation, and this had the major advantage of enabling organisms to adapt to changing environments. Sex did, however, come with a cost. In reproducing asexually, no time nor energy needs to be expended in choosing a mate. And if the environment has not changed, then there may be little reason for variation, as the organism may already be well adapted. Sex, however, has evolved as the most prolific means of species branching into the tree of life. Diversification into the phylogenetic tree happens much more rapidly via sexual reproduction than it does by way of asexual reproduction.

Evolution of sexual reproduction describes how sexually reproducing animals, plants, fungi and protists could have evolved from a common ancestor that was a single-celled eukaryotic species (Letunic & Bork, 2006, 2007, 2011). Sexual reproduction is widespread in the Eukarya, though a few eukaryotic species have secondarily lost the ability to reproduce sexually, such as Bdelloidea, and some plants and animals routinely reproduce asexually (by apomixis and parthenogenesis) without entirely having lost sex. The evolution of sex contains two related yet distinct themes: its *origin* and its *maintenance*.

The origin of sexual reproduction can be traced to early prokaryotes, around two billion years ago (Gya), when bacteria began exchanging genes via conjugation, transformation, and transduction (Otto, 2014). Though these processes are distinct from true sexual reproduction, they share some basic similarities. In eukaryotes, true sex is thought to have arisen in the Last Eukaryotic Common Ancestor (LECA), possibly via several processes of varying success, and then to have persisted (compare to "LUCA - Last Universal Common Ancestor," referring to ancestry shared by plants, animals, and bacteria) (Goodenough & Heitman, 2014).

Since hypotheses for the origin of sex are difficult to verify experimentally (outside of evolutionary computation), most current work has focused on the persistence of sexual reproduction over evolutionary time. The maintenance of sexual reproduction (specifically, of its dioecious form) by natural selection in a highly competitive world has long been one of the major mysteries of biology, since both other known mechanisms of reproduction – asexual reproduction and hermaphroditism – possess apparent advantages over it. Asexual reproduction can proceed by budding, fission, or spore formation and does not involve the union of gametes, which accordingly results in a much faster rate of reproduction compared to sexual reproduction, where 50% of offspring are males and unable to produce offspring themselves. In hermaphroditic reproduction, each of the two parent organisms required for the formation of a zygote can provide either the male or the female gamete, which leads to advantages in both size and genetic variance of a population.

Sexual reproduction therefore must offer significant fitness advantages because, despite the two-fold cost of sex (see below), it dominates among multicellular forms of life, implying that the fitness of offspring produced by sexual processes outweighs the costs. Sexual reproduction derives from recombination, where parent genotypes are reorganized and shared with the offspring. This stands in contrast to single-parent asexual replication, where the offspring is always identical to the parents (barring mutation). Recombination supplies two fault-tolerance mechanisms at the molecular level: *recombinational DNA repair* (promoted during meiosis because homologous chromosomes pair at that time) and *complementation* (also known as heterosis, hybrid vigor or masking of mutations).



Figure 12.1.6**:** Ladybugs mating; Pollen production is an essential step in sexual reproduction of seed plants.

Historical Perspective

The issue of the evolution of sexual reproduction features in the writings of Aristotle, and modern philosophical-scientific thinking on the problem dates from at least Erasmus Darwin (1731–1802) in the 18th century. August Weismann picked up the thread in 1889, arguing that sex serves to generate genetic variation, as detailed in the majority of the explanations below. On the other hand, Charles Darwin (1809–1882) concluded that the effect of hybrid vigor (complementation) "is amply sufficient to account for the ...

genesis of the two sexes". This is consistent with the repair and complementation hypothesis, described below. Since the emergence of the modern evolutionary synthesis in the 20th century, numerous biologists including W. D. Hamilton, Alexey Kondrashov, George C. Williams, Harris Bernstein, Carol Bernstein, Michael M. Cox, Frederic A. Hopf and Richard E. Michod – have suggested competing explanations for how a vast array of different living species maintain sexual reproduction.

Disadvantages of Sex and Sexual Reproduction

The paradox of the existence of sexual reproduction is that though it is ubiquitous in multicellular organisms, there are ostensibly many inherent disadvantages to reproducing sexually when weighed against the relative advantages of alternative forms of reproduction, such as asexual reproduction. Thus, because sexual reproduction abounds in complex multicellular life, there must be some significant benefit(s) to sex and sexual reproduction that compensates for these fundamental disadvantages.

Population Expansion Cost of Sex

Among the most limiting disadvantages to the evolution of sexual reproduction by natural selection is that an asexual population can grow much more rapidly than a sexual one with each generation.

For example, assume that the entire population of some theoretical species has 100 total organisms consisting of two sexes (i.e. males and females), with 50:50 male-to-female representation, and that only the females of this species can bear offspring. If all capable members of this population procreated once, a total of 50 offspring would be produced (the *F1* generation). Contrast this outcome with an asexual species, in which each and every member of an equally sized 100-organism population is capable of bearing young. If all capable members of this asexual population procreated once, a total of 100 offspring would be produced – twice as many as produced by the sexual population in a single generation.

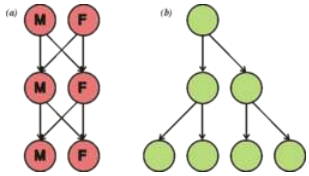


Figure 12.1.7**:** This diagram illustrates the *two-fold cost of sex*. If each individual were to contribute to the same number of offspring (two), *(a)* the sexual population remains the same size each generation, where the *(b)* asexual population doubles in size each generation.

This idea is sometimes referred to as the **two-fold cost of sexual reproduction**. It was first described mathematically by John Maynard Smith (1978). In his manuscript, Smith further speculated on the impact of an asexual mutant arising in a sexual population, which suppresses meiosis and allows eggs to develop into offspring genetically identical to the mother by mitotic division (Stearns, 2005). The mutant-asexual lineage would double its representation in the population each generation, all else being equal.

Technically the problem above is not one of sexual reproduction but of having a subset of organisms incapable of bearing offspring. Indeed, some multicellular organisms (isogamous) engage in sexual reproduction but all members of the species are capable of bearing offspring (Hoekstra, 1987). The two-fold reproductive disadvantage assumes that males contribute only genes to their offspring and sexual females waste half their reproductive potential on sons (Stearns, 2005). Thus, in this formulation, the principal cost of sex is that males and females must successfully copulate, which almost always involves expending energy to come together through time and space. Asexual organisms do not need to expend the energy necessary to find a mate.

Genetic Heritability Cost of Sex

A sexually reproducing organism only passes on ~50% of its own genetic material to each offspring. This is a consequence of the fact that gametes from sexually reproducing species are haploid. Again, however, this is not applicable to all sexual organisms. There are numerous species which are sexual but do not have a genetic-loss problem because they do not produce males or females. Yeast, for example, are isogamous sexual organisms which have two mating types which fuse and recombine their haploid genomes. Both sexes reproduce during the haploid and diploid stages of their life cycle and have a 100% chance of passing their genes into their offspring (Hoekstra, 1987).

Some species avoid the 50% cost of sexual reproduction, although they have "sex" (in the sense of genetic recombination). In these species (e.g., bacteria, ciliates, dinoflagellates and diatoms), "sex" and reproduction occurs separately (Ridley, 2003; Beukeboom & Perrin, 2014).

Advantages of Sex and Sexual Reproduction

The concept of sex includes two fundamental phenomena: the sexual process (fusion of genetic information of two individuals) and sexual differentiation (separation of this information into two parts). Depending on the presence or absence of these phenomena, all of the existing forms of reproduction can be classified as asexual, hermaphrodite or dioecious. The sexual process and sexual differentiation are different phenomena, and, in essence, are diametrically opposed. The first creates (increases) diversity of genotypes, and the second decreases it by half.

Reproductive advantages of the asexual forms are in quantity of the progeny, and the advantages of the hermaphrodite forms are in maximal diversity. Transition from the hermaphrodite to dioecious state leads to a loss of at least half of the diversity. So, the primary challenge is to explain the advantages given by sexual differentiation, i.e. the benefits of two separate sexes compared to hermaphrodites rather than to explain benefits of sexual forms (hermaphrodite + dioecious) over asexual ones. It has already been understood that since sexual reproduction is not associated with any clear reproductive advantages, as compared with asexual, there should be some important advantages in evolution (Crow, 1994).

Advantages Due to Genetic Variation

For the advantage due to genetic variation, there are three possible reasons this might happen. First, sexual reproduction can combine the effects of two beneficial mutations in the same individual (i.e. **sex aids in the spread of advantageous traits**). Also, the necessary mutations do not have to have occurred one after another in a single line of descendants (Goldstein, 2010). Second, sex acts to bring together currently deleterious mutations to create severely unfit individuals that are then eliminated from the population (i.e. **sex aids in the removal of deleterious genes**). However, in organisms containing only one set of chromosomes, deleterious mutations would be eliminated immediately, and therefore removal of harmful mutations is an unlikely benefit for sexual reproduction. Lastly, **sex creates new gene combinations that may be more fit** than previously existing ones, or may simply lead to reduced competition among relatives.

For the advantage due to DNA repair, there is an immediate large benefit of removing DNA damage by recombinational DNA repair during meiosis, since this removal allows greater survival of progeny with undamaged DNA. The advantage of complementation to each sexual partner is avoidance of the bad effects of their deleterious recessive genes in progeny by the masking effect of normal dominant genes contributed by the other partner.

The classes of hypotheses based on the creation of variation are further broken down below. Any number of these hypotheses may be true in any given species (they are not mutually exclusive), and different hypotheses may apply in different species. However, a research framework based on creation of variation has yet to be found that allows one to determine whether the reason for sex is universal for all sexual species, and, if not, which mechanisms are acting in each species.

On the other hand, the maintenance of sex based on DNA repair and complementation applies widely to all sexual species.

Protection from Major Genetic Mutation

In contrast to the view that sex promotes genetic variation, Heng, and Gorelick and Heng reviewed evidence that sex actually acts as a constraint on genetic variation (2007; 2011). They consider that sex acts as a coarse filter, weeding out major genetic changes, such as chromosomal rearrangements, but permitting minor variation, such as changes at the nucleotide or gene level (that are often neutral) to pass through the sexual sieve.

Novel Genotypes

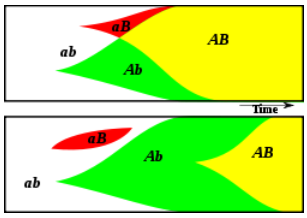


Figure 12.1.8**:** This diagram illustrates how sex might create novel genotypes more rapidly. Two advantageous alleles *A* and *B* occur at random. The two alleles are recombined rapidly in a sexual population (top), but in an asexual population (bottom) the two alleles must independently arise because of clonal interference.

Sex could be a method by which novel genotypes are created. Because sex combines genes from two individuals, sexually reproducing populations can more easily combine advantageous genes than can asexual populations. If, in a sexual population, two different advantageous alleles arise at different loci on a chromosome in different members of the population, a chromosome containing the two advantageous alleles can be produced within a few generations by recombination. However, should the same two alleles arise in different members of an asexual population, the only way that one chromosome can develop the other allele is to independently gain the same mutation, which would take much longer. Several studies have addressed counterarguments, and the question of whether this model is sufficiently robust to explain the predominance of sexual versus asexual reproduction remains (Birdsell & Wills, 2003).

Ronald Fisher also suggested that sex might facilitate the spread of advantageous genes by allowing them to better escape their genetic surroundings, if they should arise on a chromosome with deleterious genes.

Supporters of these theories respond to the balance argument that the individuals produced by sexual and asexual reproduction may differ in other respects too – which may influence the persistence of sexuality. For example, in the heterogamous water fleas of the genus *Cladocera*, sexual offspring form eggs which are better able to survive the winter versus those the fleas produce asexually.

Increased Resistance to Parasites

One of the most widely discussed theories to explain the persistence of sex is that it is maintained to assist sexual individuals in resisting parasites, also known as the **Red Queen Hypothesis** (Birdsell & Wills, 2003; Ridley, 1995; MacIntyre & Clegg, 2003; Van Valen, 1973; Hamilton et al., 1990).

When an environment changes, previously neutral or deleterious alleles can become favorable. If the environment changed sufficiently rapidly (i.e. between generations), these changes in the environment can make sex advantageous for the individual. Such rapid changes in environment are caused by the co-evolution between hosts and parasites.

Imagine, for example that there is one gene in parasites with two alleles *p* and *P* conferring two types of parasitic ability, and one gene in hosts with two alleles *h* and *H*, conferring two types of parasite resistance, such that parasites with allele *p* can attach themselves to hosts with the allele *h*, and *P* to *H*. Such a situation will lead to cyclic changes in allele frequency – as *p* increases in frequency, *h* will be disfavored.

In reality, there will be several genes involved in the relationship between hosts and parasites. In an asexual population of hosts, offspring will only have the different parasitic resistance if a mutation arises. In a sexual population of hosts, however, offspring will have a new combination of parasitic resistance alleles.

In other words, like Lewis Carroll's Red Queen, sexual hosts are continually "running" (adapting) to "stay in one place" (resist parasites).

Evidence for this explanation for the evolution of sex is provided by comparison of the rate of molecular evolution of genes for kinases and immunoglobulins in the immune system with genes coding other proteins. The genes coding for immune system proteins evolve considerably faster (Kuma et al., 1995; Wolfe & Sharp, 1993).

Further evidence for the Red Queen hypothesis was provided by observing long-term dynamics and parasite coevolution in a "mixed" (sexual and asexual) population of snails (*Potamopyrgus antipodarum*). The number of sexuals, the number of asexuals, and the rates of parasite infection for both were monitored. It was found that clones that were plentiful at the beginning of the study became more susceptible to parasites over time. As parasite infections increased, the once plentiful clones dwindled dramatically in

number. Some clonal types disappeared entirely. Meanwhile, sexual snail populations remained much more stable over time (Jokela, 2009; Parasties may have had a role, 2009).

However, Hanley et al. studied mite infestations of a parthenogenetic gecko species and its two related sexual ancestral species (1995). Contrary to expectation based on the Red Queen hypothesis, they found that the prevalence, abundance and mean intensity of mites in sexual geckos was significantly higher than in asexuals sharing the same habitat.

In 2011, researchers used the microscopic roundworm *Caenorhabditis elegans* as a host and the pathogenic bacteria *Serratia marcescens* to generate a host-parasite coevolutionary system in a controlled environment, allowing them to conduct more than 70 evolution experiments testing the Red Queen Hypothesis. They genetically manipulated the mating system of *C. elegans*, causing populations to mate either sexually, by self-fertilization, or a mixture of both within the same population. Then they exposed those populations to the *S. marcescens* parasite. It was found that the self-fertilizing populations of *C. elegans* were rapidly driven extinct by the coevolving parasites while sex allowed populations to keep pace with their parasites, a result consistent with the Red Queen Hypothesis (Morran et al., 2011; Science Daily, 2011). In natural populations of *C. elegans*, self-fertilization is the predominant mode of reproduction, but infrequent out-crossing events occur at a rate of about 1% (Barrière & Félix, 2005).

DNA Repair and Complementation

The repair and complementation hypothesis assumes that genetic recombination is fundamentally a DNA repair process, and that when it occurs during meiosis it is an adaptation for repairing the genomic DNA which is passed on to progeny. Recombinational repair is the only repair process known which can accurately remove double-strand damages in DNA, and such damages are both common in nature and ordinarily lethal if not repaired. For instance, double-strand breaks in DNA occur about 50 times per cell cycle in human cells (naturally occurring DNA damage). Recombinational repair is prevalent from the simplest viruses to the most complex multicellular eukaryotes. It is effective against many different types of genomic damage, and in particular is highly efficient at overcoming double-strand damages. Studies of the mechanism of meiotic recombination indicate that meiosis is an adaptation for repairing DNA (Cox, 2001). These considerations form the basis for the first part of the repair and complementation hypothesis.

In some lines of descent from the earliest organisms, the diploid stage of the sexual cycle, which was at first transient, became the predominant stage, because it allowed complementation — the masking of deleterious recessive mutations (i.e. hybrid vigor or heterosis). Outcrossing, the second fundamental aspect of sex, is maintained by the advantage of masking mutations and the disadvantage of inbreeding (mating with a close relative) which allows expression of recessive mutations (commonly observed as inbreeding depression). This is in accord with Charles Darwin, who concluded that the adaptive advantage of sex is hybrid vigor; or as he put it, "the offspring of two individuals, especially if their progenitors have been subjected to very different conditions, have a great advantage in height, weight, constitutional vigor and fertility over the self fertilized offspring from either one of the same parents," (1876).

However, outcrossing may be abandoned in favor of parthenogenesis or selfing (which retain the advantage of meiotic recombinational repair) under conditions in which the costs of mating are very high. For instance, costs of mating are high when individuals are rare in a geographic area, such as when there has been a forest fire and the individuals entering the burned area are the initial ones to arrive. At such times mates are hard to find, and this favors parthenogenic species.

In the view of the repair and complementation hypothesis, the removal of DNA damage by recombinational repair produces a new, less deleterious form of informational noise, allelic recombination, as a by-product. This lesser informational noise generates genetic variation, viewed by some as the major effect of sex.

Deleterious Mutation Clearance

Mutations can have many different effects upon an organism. It is generally believed that the majority of non-neutral mutations are deleterious, which means that they will cause a decrease in the organism's overall fitness (Griffiths, et al., 1999). If a mutation has a deleterious effect, it will then usually be removed from the population by the process of natural selection. Sexual reproduction is believed to be more efficient than asexual reproduction in removing those mutations from the genome (Kondrashov, 1988).

There are two main hypotheses which explain how sex may act to remove deleterious genes from the genome.

Evading Harmful Mutation Build-up

While DNA is able to recombine to modify alleles, DNA is also susceptible to mutations within the sequence that can affect an organism in a negative manner. Asexual organisms do not have the ability to recombine their genetic information to form new and differing alleles. Once a mutation occurs in the DNA or other genetic carrying sequence, there is no way for the mutation to be removed from the population until another mutation occurs that ultimately deletes the primary mutation. This is rare among organisms.

Hermann Joseph Muller introduced the idea that mutations build up in asexual reproducing organisms. Muller described this occurrence by comparing the mutations that accumulate as a ratchet. Each mutation that arises in asexually reproducing organisms turns the ratchet once. The ratchet is unable to be rotated backwards, only forwards. The next mutation that occurs turns the ratchet once more. Additional mutations in a population continually turn the ratchet and the mutations, mostly deleterious, continually accumulate without recombination (Muller, 1964). These mutations are passed onto the next generation because the offspring are exact genetic clones of their parents. The genetic load of organisms and their populations will increase due to the addition of multiple deleterious mutations and decrease the overall reproductive success and fitness.

Removal of Deleterious Genes

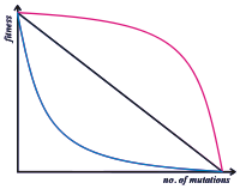


Figure 12.1.9**:** Diagram illustrating different relationships between numbers of mutations and fitness. Kondrashov's model requires *synergistic epistasis*, which is represented by the red line – each subsequent mutation has a disproportionately large effect on the organism's fitness (Ridley, 2004; Charlesworth & Charlesworth, 2010).

This hypothesis was proposed by Alexey Kondrashov, and is sometimes known as the *deterministic mutation hypothesis* (1988). It assumes that the majority of deleterious mutations are only slightly deleterious, and affect the individual such that the introduction of each additional mutation has an increasingly large effect on the fitness of the organism. This relationship between number of mutations and fitness is known as *synergistic epistasis*.

By way of analogy, think of a car with several minor faults. Each is not sufficient alone to prevent the car from running, but in combination, the faults combine to prevent the car from functioning.

Similarly, an organism may be able to cope with a few defects, but the presence of many mutations could overwhelm its backup mechanisms.

Kondrashov argues that the slightly deleterious nature of mutations means that the population will tend to be composed of individuals with a small number of mutations. Sex will act to recombine these genotypes, creating some individuals with fewer deleterious mutations, and some with more. Because there is a major selective disadvantage to individuals with more mutations, these individuals die out. In essence, sex compartmentalizes the deleterious mutations.

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Contributors and Attributions

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12.2: Sex determination and sex ratios

Sex determination

A **sex-determination system** is a biological system that determines the development of sexual characteristics in an organism. Most organisms that create their offspring using sexual reproduction have two sexes.

In some species there are hermaphrodites (Rosenfield, 2018). There are also some species that are only one sex due to parthenogenesis, the act of a female reproducing without fertilization.

In many species, sex determination is genetic: males and females have different alleles or even different genes that specify their sexual morphology. In animals this is often accompanied by chromosomal differences, generally through combinations of XY, ZW, XO, ZO chromosomes, or haplodiploidy. The sexual differentiation is generally triggered by a main gene (a "sex locus"), with a multitude of other genes following in a domino effect.

In other cases, sex of a fetus is determined by environmental variables (such as temperature). The details of some sex-determination systems are not yet fully understood.

Some species such as various plants and fish do not have a fixed sex, and instead go through life cycles and change sex based on genetic cues during corresponding life stages of their type. This could be due to environmental factors such as seasons, temperature, or even social context. In some gonochoric species, a few individuals may have sex characteristics of both sexes, a condition called intersex (Minelli & Fusco, 2019).

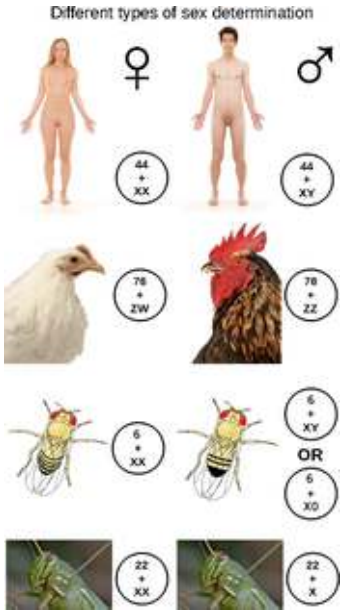


Figure 12.2.1**:** Some chromosomal sex determination systems in animals.

Discovery

Sex determination was discovered in the mealworm by the American geneticist Nettie Stevens in 1903 (Nature Education, n.d.; Ogilvie & Choquette, 1981; Smith, 2010).



Figure 12.2.2**:** Nettie Stevens.

Chromosomal systems

XX/XY sex chromosomes

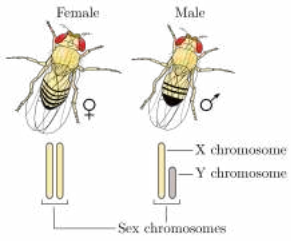


Figure 12.2.3**:** Drosophila sex-chromosomes.

The **XX/XY sex-determination system** is the most familiar, as it is found in humans. The XX/XY system is found in most other mammals, as well as some insects. In this system, most females have two of the same kind of sex chromosome (XX), while most males have two distinct sex chromosomes (XY). The X and Y sex chromosomes are different in shape and size from each other, unlike the rest of the chromosomes (autosomes), and are sometimes called allosomes. In some species, such as humans, organisms remain sex indifferent for a period of time after fertilization; in others, however, such as fruit flies, sexual differentiation occurs as soon as the egg is fertilized (Hake, 2008).

X-centered sex determination

Some species, such as fruit flies, use the presence of two X chromosomes to determine femaleness (Penalva & Sánchez, 2003). Species that use the number of Xs to determine sex are nonviable with an extra X chromosome.

XX/X0 sex chromosomes

In this variant of the XY system, females have two copies of the sex chromosome (XX) but males have only one (X0). The *0* denotes the absence of a second sex chromosome. Generally in this method, the sex is determined by amount of genes expressed across the two chromosomes. This system is observed in a number of insects, including the grasshoppers and crickets of order Orthoptera and in cockroaches (order Blattodea). A small number of mammals also lack a Y chromosome. These include the Amami spiny rat (*Tokudaia osimensis*) and the Tokunoshima spiny rat (*Tokudaia tokunoshimensis*) and *Sorex araneus*, a shrew species. Transcaucasian mole voles (*Ellobius lutescens*) also have a form of XO determination, in which both sexes lack a second sex chromosome (Chandra, 1999). The mechanism of sex determination is not yet understood (Kuroiwa et al., 2011).

The nematode *C. elegans* is male with one sex chromosome (X0); with a pair of chromosomes (XX) it is a hermaphrodite (Majerus, 2003, p. 60). Its main sex gene is XOL, which encodes XOL-1 and also controls the expression of the genes TRA-2 and HER-1. These genes reduce male gene activation and increase it, respectively (Kuwabara et al., 1992).

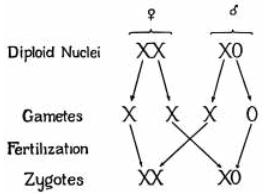


Figure 12.2.4**:** Heredity of sex chromosomes in XO sex determination.

ZW/ZZ sex chromosomes

The **ZW sex-determination system** is found in birds, some reptiles, and some insects and other organisms. The ZW sex-determination system is reversed compared to the XY system: females have two different kinds of chromosomes (ZW), and males have two of the same kind of chromosomes (ZZ). In the chicken, this was found to be dependent on the expression of DMRT1 (Smith et al., 2009). In birds, the genes FET1 and ASW are found on the W chromosome for females, similar to how the Y

chromosome contains SRY (Hake, 2008). However, not all species depend upon the W for their sex. For example, there are moths and butterflies that are ZW, but some have been found female with ZO, as well as female with ZZW (Majerus, 2003, p. 60). Also, while mammals deactivate one of their extra X chromosomes when female, it appears that in the case of Lepidoptera, the males produce double the normal amount of enzymes, due to having two Z's (Majerus, 2003, p. 60). Because the use of ZW sex determination is varied, it is still unknown how exactly most species determine their sex (Majerus, 2003, p. 60). However, reportedly, the silkworm *Bombyx mori* uses a single female-specific piRNA as the primary determiner of sex (Kiuchi et al., 2014). Despite the similarities between the ZW and XY systems, these sex chromosomes evolved separately. In the case of the chicken, their Z chromosome is more similar to humans' autosome 9 (Stiglec et al., 2007). The chicken's Z chromosome also seems to be related to the X chromosome of the platypus (Grützner, 2004). When a ZW species, such as the Komodo dragon, reproduces parthenogenetically, usually only males are produced. This is due to the fact that the haploid eggs double their chromosomes, resulting in ZZ or WW. The ZZ become males, but the WW are not viable and are not brought to term (BBC News, 2006).

In both XY and ZW sex determination systems, the sex chromosome carrying the critical factors is often significantly smaller, carrying little more than the genes necessary for triggering the development of a given sex (Annenberg Media, 2004).

Haplodiploidy

Haplodiploidy is found in insects belonging to Hymenoptera, such as ants and bees. Sex determination is controlled by the zygosity of a complementary sex determiner (*csd*) locus. Unfertilized eggs develop into haploid individuals which have a single, hemizygous copy of the *csd* locus and are therefore males. Fertilized eggs develop into diploid individuals which, due to high variability in the *csd* locus, are generally heterozygous females. In rare instances diploid individuals may be homozygous, these develop into sterile males. The gene acting as a *csd* locus has been identified in the honeybee and several candidate genes have been proposed as a *csd* locus for other Hymenopterans (Beye et al., 2003; Privman, 2013; Miyakawa, 2018). Most females in the Hymenoptera order can decide the sex of their offspring by holding received sperm in their spermatheca and either releasing it into their oviduct or not. This allows them to create more workers, depending on the status of the colony (Van Wilgenburg, 2006).

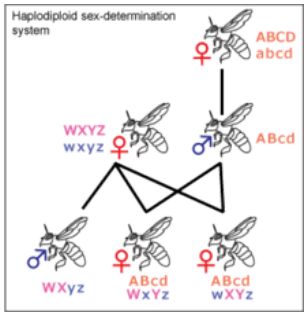


Figure 12.2.5**:** Haplodiploid sex chromosomes.

Environmental systems

Temperature-dependent

Many other sex-determination systems exist. In some species of reptiles, including alligators, some turtles, and the tuatara, sex is determined by the temperature at which the egg is incubated during a temperature-sensitive period. There are no examples of temperature-dependent sex determination (TSD) in birds. Megapodes had formerly been thought to exhibit this phenomenon, but were found to actually have different temperature-dependent embryo mortality rates for each sex (Göth & Booth, 2005). For some species with TSD, sex determination is achieved by exposure to hotter temperatures resulting in the offspring being one sex and cooler temperatures resulting in the other. This type of TSD is called *Pattern I*. For others species using TSD, it is exposure to temperatures on both extremes that results in offspring of one sex, and exposure to moderate temperatures that results in offspring of the opposite sex, called *Pattern II* TSD. The specific temperatures required to produce each sex are known as the female-promoting temperature and the male-promoting temperature (Torres Maldonado et al, 2002). When the temperature stays near the threshold during the temperature sensitive period, the sex ratio is varied between the two sexes (Bull, 1980). Some species' temperature standards are based on when a particular enzyme is created. These species that rely upon temperature for their sex determination do not have the SRY gene, but have other genes such as DAX1, DMRT1, and SOX9 that are expressed or not expressed depending on the temperature (Torres Maldonado et al., 2002). The sex of some species, such as the Nile tilapia,

Australian skink lizard, and Australian dragon lizard, is initially determined by chromosomes, but can later be changed by the temperature of incubation (Schartl, 2004).

It is unknown how exactly temperature-dependent sex determination evolved (Valenzuela & Janzen, 2001). It could have evolved through certain sexes being more suited to certain areas that fit the temperature requirements. For example, a warmer area could be more suitable for nesting, so more females are produced to increase the amount that nest next season (Valenzuela & Janzen, 2001). Environmental sex determination preceded the genetically determined systems of birds and mammals; it is thought that a temperature-dependent amniote was the common ancestor of amniotes with sex chromosomes (Janzen & Phillips, 2006).



Figure 12.2.6**:** All alligators determine the sex of their offspring by the temperature of the nest.

Other systems

There are other environmental sex determination systems including location-dependent determination systems as seen in the marine worm *Bonellia viridis* – larvae become males if they make physical contact with a female, and females if they end up on the bare sea floor. This is triggered by the presence of a chemical produced by the females, bonellin (Gilbert, 2006). Some species, such as some snails, practice sex change: adults start out male, then become female. In tropical clown fish, the dominant individual in a group becomes female while the other ones are male, and bluehead wrasses (*Thalassoma bifasciatum*) are the reverse. Some species, however, have no sex-determination system. Hermaphrodite species include the common earthworm and certain species of snails. A few species of fish, reptiles, and insects reproduce by parthenogenesis and are female altogether. There are some reptiles, such as the boa constrictor and Komodo dragon that can reproduce both sexually and asexually, depending on whether a mate is available (Watts et al., 2006).

Other unusual systems include those of the green swordtail (a polyfactorial system with the sex-determining genes on several chromosomes); the juvenile hermaphroditism of zebrafish, with an unknown trigger; and the platyfish, which has W, X, and Y chromosomes. This allows WY, WX, or XX females and YY or XY males (Schartl, 2004).

Sex ratios

The **sex ratio** is the ratio of males to females in a population. In most sexually reproducing species, the ratio tends to be 1:1. This tendency is explained by Fisher's principle (Hamilton, 1967). For various reasons, however, many species deviate from anything like an even sex ratio, either periodically or permanently. Examples include parthenogenic species, periodically mating organisms such as aphids, some eusocial wasps such as *Polistes fuscatus* and *Polistes exclamans*, bees, ants, and termites (Kobayashi et al., 2013). In most species, the sex ratio varies according to the age profile of the population (Coney & Mackey, 1998).

Fisher's principle

Fisher’s principle explains why for most species, the sex ratio is approximately 1:1. Bill Hamilton expounded Fisher’s argument in his 1967 paper on “Extraordinary sex ratios” as follows, given the assumption of equal parental expenditure on offspring of both sexes (Hamilton, 1967).

1. Suppose male births are less common than female.
2. A newborn male then has better mating prospects than a newborn female, and therefore can expect to have more offspring.
3. Therefore parents genetically disposed to produce males tend to have more than average numbers of grandchildren born to them.
4. Therefore the genes for male-producing tendencies spread, and male births become more common.
5. As the 1:1 sex ratio is approached, the advantage associated with producing males dies away.
6. The same reasoning holds if females are substituted for males throughout. Therefore 1:1 is the equilibrium ratio.

In modern language, the 1:1 ratio is the evolutionarily stable strategy (ESS) (Smith & Price, 1973). This ratio has been observed in many species, including the bee *Macrotera portalis*. A study performed by Danforth observed no significant difference in the number of males and females from the 1:1 sex ratio (Danforth, 1991).

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12.3: Mating systems in sexual animals

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Mating systems in sexual animals

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12.4: Mating Systems in Plants

Asexual Reproduction

Many plants are facultatively sexual rather than obligately sexual. Asexual reproduction is a type of reproduction where the offspring comes from one parent only, thus, inheriting the characteristics of the parent. Asexual reproduction in plants occurs in two fundamental forms vegetative reproduction and agamospermy (Barrett, 2008). Vegetative reproduction involves a vegetative piece of the original plant producing new individuals by budding, tillering, etc. and is distinguished from apomixis, which is a replacement of sexual reproduction, and in some cases involves seeds. Apomixis occurs in many plant species such as dandelions (*Taraxacum* species) and also in some non-plant organisms. For apomixis and similar processes in non-plant organisms, see parthenogenesis.

Natural vegetative reproduction is a process mostly found in perennial plants, and typically involves structural modifications of the stem or roots and in a few species leaves. Most plant species that employ vegetative reproduction do so as a means to perennialize the plants, allowing them to survive from one season to the next and often facilitating their expansion in size. A plant that persists in a location through vegetative reproduction of individuals constitutes a clonal colony. A single ramet, or apparent individual, of a clonal colony is genetically identical to all others in the same colony. The distance that a plant can move during vegetative reproduction is limited, though some plants can produce ramets from branching rhizomes or stolons that cover a wide area, often in only a few growing seasons. In a sense, this process is not one of reproduction but one of survival and expansion of biomass of the individual. When an individual organism increases in size via cell multiplication and remains intact, the process is called vegetative growth. However, in vegetative reproduction, the new plants that result are new individuals in almost every respect except genetic. A major disadvantage of vegetative reproduction, is the transmission of pathogens from parent to offspring. It is uncommon for pathogens to be transmitted from the plant to its seeds (in sexual reproduction or in apomixis), though there are occasions when it occurs (Fritz & Simms, 1992).

Seeds generated by apomixis are a means of asexual reproduction, involving the formation and dispersal of seeds that do not originate from the fertilization of the embryos. Hawkweeds (*Hieracium*), dandelions (*Taraxacum*), some species of *Citrus* and Kentucky blue grass (*Poa pratensis*) all use this form of asexual reproduction. Pseudogamy occurs in some plants that have apomictic seeds, where pollination is often needed to initiate embryo growth, though the pollen contributes no genetic material to the developing offspring (O'Neill, 2003). Other forms of apomixis occur in plants also, including the generation of a plantlet in replacement of a seed or the generation of bulbils instead of flowers, where new cloned individuals are produced.

Sexual Reproduction

Sexual reproduction involves two fundamental processes: meiosis, which rearranges the genes and reduces the number of chromosomes, and fertilisation, which restores the chromosome to a complete diploid number. In between these two processes, different types of plants and algae vary, but many of them, including all land plants, undergo alternation of generations, with two different multicellular structures (phases), a gametophyte and a sporophyte.

In mosses and liverworts, the gametophyte is relatively large, and the sporophyte is a much smaller structure that is never separated from the gametophyte. In ferns, gymnosperms, and flowering plants (angiosperms), the gametophytes are relatively small and the sporophyte is much larger. In gymnosperms and flowering plants the megagametophyte is contained within the ovule (that may develop into a seed) and the microgametophyte is contained within a pollen grain.

In the evolution of early plants, abiotic means, including water and much later, wind, transported sperm for reproduction. The first plants were aquatic, and released sperm freely into the water to be carried with the currents. Ancestral land plants like liverworts and mosses have motile sperm that swam in a thin film of water or were splashed in water droplets. As taller and more complex plants evolved, modifications in the alternation of generations evolved. In the Paleozoic era progymnosperms reproduced by using spores dispersed on the wind and many gymnosperms and some angiosperms still rely on wind for gamete dispersal. The seed plants including seed ferns, conifers and cordaites have pollen grains that contain the male gametes for protection of the sperm during the process of transfer from the male to female parts. Angiosperms, or flowering plants, are the most derived and most abundant plant species and they rely on flowers producing pollen and ovules for reproduction.

Self-Fertilization and Self-Incompatibility

Many species of plants, particularly those which produce both staminate and pistillate flowers or produce 'perfect' bisexual flowers, also have the ability to reproduce sexually with themselves. This is advantageous particularly if pollination services are unreliable or unpredictable, as it ensures the plant still has some fitness. **Self-pollination** is a form of pollination in which pollen from the same plant arrives at the stigma of a flower (in flowering plants) or at the ovule (in gymnosperms). The term **selfing** that is often used as a synonym, is not limited to self-pollination, but also applies to other types of self-fertilization. Plants may either be obligately self-fertilizing, or facultatively so. In facultatively selfing plants, there may be mechanisms which delay selfing, such as stamens that are initially reflexed but move to come into contact with the stigma. About 42% of flowering plants exhibit a mixed mating system in nature (Goodwillie et al., 2005). In the most common kind of system, individual plants produce a single flower type and fruits may contain self-pollinated, out-crossed or a mixture of progeny types. Another mixed mating system is referred to as dimorphic cleistogamy. In this system a single plant produces both open, potentially out-crossed and closed, obligately self-pollinated cleistogamous flowers (Munguía-Rosas et al., 2013).

Still other species are self-incompatible, and will reject their own pollen grains if they land on their own stigmatic surface. These plants are obligately outcrossing, and must successfully sexually reproduce with another member of their species. In plants with SI, when a pollen grain produced in a plant reaches a stigma of the same plant or another plant with a matching allele or genotype, the process of pollen germination, pollen-tube growth, ovule fertilization, or embryo development is inhibited, and consequently no seeds are produced. SI is one of the most important means of preventing inbreeding and promoting the generation of new genotypes in plants and it is considered one of the causes of the spread and success of angiosperms on the earth.

Outcrossing Fertilization

Plants that use insects or other animals to move pollen from one flower to the next have developed greatly modified flower parts to attract pollinators and to facilitate the movement of pollen from one flower to the insect and from the insect back to the next flower. Flowers of wind-pollinated plants tend to lack petals and or sepals; typically large amounts of pollen are produced and pollination often occurs early in the growing season before leaves can interfere with the dispersal of the pollen. Many trees and all grasses and sedges are wind-pollinated.

Plants have a number of different means to attract pollinators including color, scent, heat, nectar glands, edible pollen and flower shape. Along with modifications involving the above structures two other conditions play a very important role in the sexual reproduction of flowering plants, the first is the timing of flowering and the other is the size or number of flowers produced. Often plant species have a few large, very showy flowers while others produce many small flowers, often flowers are collected together into large inflorescences to maximize their visual effect, becoming more noticeable to passing pollinators. Flowers are attraction strategies and sexual expressions are functional strategies used to produce the next generation of plants, with pollinators and plants having co-evolved, often to some extraordinary degrees, very often rendering mutual benefit. Specialization can be advantageous because it results in more consistent pollination services. As a result, the specialized pollinator and plant can exert strong selective pressure on each other, leading to coevolution. Examples of this include the coevolution between figs and fig wasps, or yucca and yucca moths, wherein the yucca moths are both the obligate pollinators and the antagonistic herbivores of yucca. Another visually striking example is the co-evolution of long floral corollas and long beaks or proboscii in pollinators 12.4.1$A + B$.

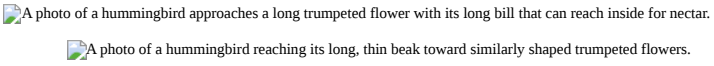


Figure 12.4.1**:** (A) Sword-billed Hummingbird in Ecuador ("Sword-Billed Hummingbird" by Andrew Morffew is licensed under CC BY 2.0); (B) Rufous Hummingbird pollinating Scarlet Gilia in the Rocky Mountains ("Rufous Hummingbird" by Smallman12q is licensed under CC BY 2.0).

Plants which share pollination methods or pollinators often accumulate suites of related traits called pollination syndromes. These have evolved in response to natural selection imposed by different pollen vectors, which can be abiotic (wind and water) or biotic, such as birds, bees, flies, etc. through a process called pollinator-mediated selection (Faegri & van der Pijl, 1980; Proctor et al., 1996). These traits include flower shape, size, colour, odor, reward type and amount, nectar composition, and timing of flowering. For example, tubular red flowers with copious nectar often attract birds; foul smelling flowers attract carrion flies or beetles, etc. Different species which use the same pollinators may either flower synchronously, to attract pollinators more successfully, or asynchronously, to avoid heterospecific pollen transfer (or stigma gunking). The latter is an example of niche partitioning.

The largest family of flowering plants is the orchids (Orchidaceae), estimated by some specialists to include up to 35,000 species, which often have highly specialized flowers that attract particular insects for pollination (Flora of North America, n.d.). The stamens are modified to produce pollen in clusters called pollinia, which become attached to insects that crawl into the flower. The flower shapes may force insects to pass by the pollen, which is "glued" to the insect. Some orchids are even more highly specialized, with flower shapes that mimic the shape of insects to attract them to attempt to 'mate' with the flowers, a few even have scents that mimic insect pheromones (12.4.2).



Figure 12.4.2**:** A bee-mimic orchid evolved to resemble a sexually receptive female bee and attract naïve male bees to pollinate it ("Bee Orchid (*Ophrys apifera*)" by Ian Capper is licensed under CC BY 2.0).

Examples of Pollination Syndromes

- Wind: Flowers may be small and inconspicuous, as well as green and not showy. They produce enormous numbers of relatively small pollen grains (hence wind-pollinated plants may be allergens, but seldom are animal-pollinated plants allergenic). Their stigmas may be large and feathery to catch the pollen grains.
- Water: Water-pollinated plants are aquatic and pollen is released into the water. Water currents therefore act as a pollen vector in a similar way to wind currents. Their flowers tend to be small and inconspicuous with many pollen grains and large, feathery stigmas to catch the pollen. However, this is relatively uncommon (only 2% of pollination is hydrophily) and most aquatic plants are insect-pollinated, with flowers that emerge into the air. *Vallisneria* is an example.
- Bee: Some bee flowers tend to be yellow or blue, often with ultraviolet nectar guides and scent. Nectar, pollen, or both are offered as rewards in varying amounts. The sugar in the nectar tends to be sucrose-dominated. A few bees collect oil from special glands on the flower (Martins et al., 2014).
- Butterfly: Butterfly-pollinated flowers tend to be large and showy, pink or lavender in colour, frequently have a landing area, and are usually scented. Since butterflies do not digest pollen (with one exception), more nectar is offered than pollen. The flowers have simple nectar guides with the nectaries usually hidden in narrow tubes or spurs, reached by the long tongue of the butterflies.
- Moth: Among the more important moth pollinators are the hawk moths (Sphingidae). Their behaviour is similar to hummingbirds: they hover in front of flowers with rapid wingbeats. Most are nocturnal or crepuscular. Moth-pollinated flowers tend to be white, night-opening, large and showy with tubular corollas and a strong, sweet scent produced in the evening, night or early morning. Much nectar is produced to fuel the high metabolic rates needed to power their flight.
- Bat: There are major differences between bat pollination in the Americas as opposed to the Afro-Eurasia. Afro-Eurasian pollinating bats are large fruit bats of the family Pteropodidae which do not have the ability to hover and must perch in the plant to lap the nectar; these bats furthermore do not have the ability to echolocate (Fleming et al., 2009). Bat-pollinated flowers in this part of the world tend to be large and showy, white or light coloured, open at night and have strong musty odours. They are often large balls of stamens. In the Americas pollinating bats are tiny creatures called glossophagines which have both the ability to hover as well as echolocate, and have extremely long tongues. Plants in this part of the world are often pollinated by

both bats and hummingbirds, and have long tubular flowers (Fleming et al., 2009). In one essay, von Helversen *et al*. speculate that maybe some bell-shaped flowers have evolved to attract bats in the Americas, as the bell-shape might reflect the sonar pulses emitted by the bats in a recognisable pattern (2003).

- Fly: Myophilous plants tend not to emit a strong scent, are typically purple, violet, blue, and white, and have open dishes or tubes (Kastinger & Weber, 2001).
- Sapromyophilous plants try to attract flies which normally visit dead animals or dung. Flowers mimic the odor of such objects. The plant provides them with no reward and they leave quickly unless it has traps to slow them down. Such plants are far less common than myophilous ones (Jones & Jones, 2001).
- Beetle: Beetle-pollinated flowers are usually large, greenish or off-white in color and heavily scented. Scents may be spicy, fruity, or similar to decaying organic material. Most beetle-pollinated flowers are flattened or dish shaped, with pollen easily accessible, although they may include traps to keep the beetle longer. The plant's ovaries are usually well protected from the biting mouthparts of their pollinators (Gullan & Cranston, 2005). A number of cantharophilous plants are thermogenic, with flowers that can increase their temperature. This heat is thought to help further spread the scent, but the infrared light produced by this heat may also be visible to insects during the dark night, and act as a shining beacon to attract them (Korotkova & Barthlott, 2009).
- Bird: Flowers pollinated by specialist nectarivores tend to be large, red or orange tubes with a lot of dilute nectar, secreted during the day. Since birds do not have a strong response to scent, they tend to be odorless. Flowers pollinated by generalist birds are often shorter and wider. Hummingbirds are often associated with pendulous flowers, whereas passerines (perching birds) need a landing platform so flowers and surrounding structures are often more robust. Also, many plants have anthers placed in the flower so that pollen rubs against the birds head/back as the bird reaches in for nectar.

…and many more!

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12.5: Sexual selection

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Sexual selection

Chapter summary

The paradox of sexual reproduction is that although it is ubiquitous in multicellular organisms, there are many disadvantages to reproducing sexually when we compare it to asexual reproduction. This chapter explores some of the multitude of hypotheses for why sexual reproduction exists, the variety of ways in which sexes are determined in plants and animals, and some of the variation in mating systems of sexual organisms. This chapter also focuses on sexual selection, a form of natural selection that occurs when traits that improve mating success are favored by selection, even if they cause a decrease in survival.

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CHAPTER OVERVIEW

Chapter 13: The Ecology of Intraspecific Variation

Learning Objectives

- Understand the difference between interspecific variation, intraspecific variation, and phenotypic plasticity
- Describe animal personality and how it is quantified
- Learn some of the current tools that ecologists use to study intraspecific variation in foraging behavior and diet

What is Intraspecific Variation?

Dog breeds vary considerably in their physical and behavioral traits, so it can be easy to forget that they are all members of the same species, *Canus familiaris* (Figure 13.1). Given their very different phenotypes, dogs like chihuahuas and great danes would play very different roles in their ecosystems if they lived in the wild. This type of variation is known as **intraspecific variation** ("within species" variation), or variation among individuals of the same species. In contrast, **interspecific variation** ("across species" variation) is variation that occurs when comparing individuals of differing species. Interspecific variation, for example, would instead refer to differences in the physical and behavioral traits of cats and dogs.



Figure 13.1: Examples of different breeds of the species *Canus familiaris.* Image is in the Public Domain.

Intraspecific variation can be attributed to pre-defined classifications (breed, age, sex) or to random differences among individuals. Anyone with two pets of the same breed, age, and sex is likely to be able to list off a variety of ways in which their pets differ whether these differences be size, temperament, or dietary preferences. These differences can be driven by genetics ("nature") and environmental factors ("nurture").

In the case of *Canus familiaris* and other domesticated species, intraspecific variation is created and maintained by artificial selection by humans. Artificial selection is not necessary for the development and maintenance of intraspecific variation, however. In natural populations, considerable variation exists between individuals of the same species for both intrinsic and extrinsic reasons, causing differences in the way that conspecifics look, behave, and respond to natural selection pressures, such as predation risk, food availability, and novel environments (Bolnick et al. 2003). This variation plays an important role in the dynamics of populations, communities, and ecosystems.

In addition to individuals varying in their average traits, ecologists are increasingly interested in how individuals vary in the flexibility of these traits. That is, how much and in what way do individuals change their behavior, morphology, physiology, or phenology in response to changing internal or external stimuli? This flexibility in behavior is known as **phenotypic plasticity** (Figure 13.2).

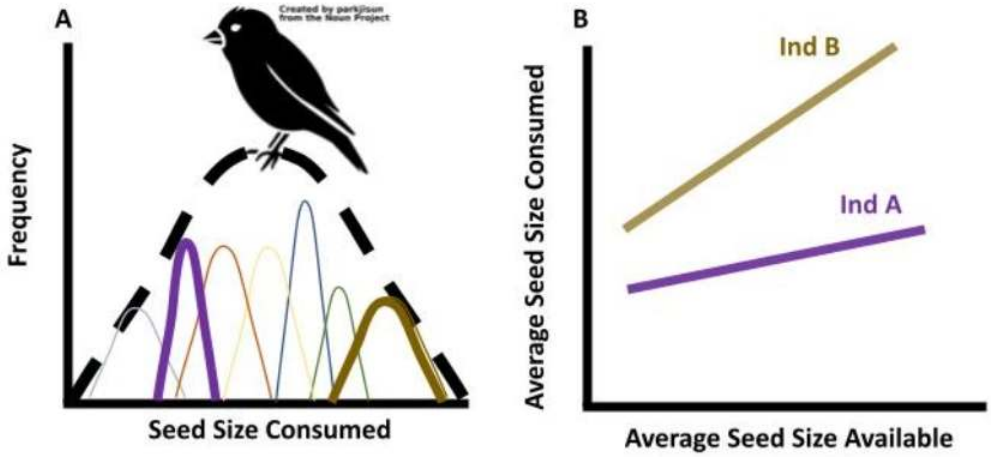


Figure 13.2: An example of intraspecific variation in a species of finch consuming seeds. Figure 13.2A depicts the overall one-dimensional niche of this species (black dashed line) in terms of the seed sizes that they consume. Within this niche, different individuals (lined of varying colors) specialize on different size seeds, showing intraspecific variation. Figure 13.2B shows how two of these individuals (Individual A and Individual B) vary their resource use with changes in resource availability. Here, Ind B shows greater phenotypic plasticity because this individual alters their resource use to a greater extent when resources change (i.e., the slope of the line for Ind B is greater).

Generally, phenotypic plasticity is more important for immobile organisms (e.g. plants) than mobile organisms (e.g. most animals), as mobile organisms can often move away from unfavorable environments (Schlichting 1968). Nevertheless, mobile organisms also have at least some degree of plasticity in at least some aspects of the phenotype. One mobile organism with substantial phenotypic plasticity is *Acyrthosiphon pisum* of the aphid family, which exhibits the ability to interchange between asexual and sexual reproduction, as well as growing wings between generations when plants become too populated (Figure 13.3) (Eisen et al. 2010).



Figure 13.3: *Acyrthosiphon pisum* by Whitney Cranshaw is Licensed under CC SA 3.0.

The Importance of Understanding Intraspecific Variation in a Changing World

Given that there is substantial variation among individuals, it is inevitable that when presented with anthropogenic stressors, individuals from the same species will respond in different ways (Bolnick et al. 2011). These varied responses may define the difference between success and failure; the likelihood of mortality or the ability to emigrate, to adapt through genetic changes, or to respond via phenotypic plasticity (Engås et al. 1996; Höglund et al. 2008; Cripps et al. 2014).

Intraspecific variation in responses can also have far-reaching impacts on the population dynamics, community structure and ecosystem function of entire groups of animals (Post et al. 2008; Rudman et al. 2015; Charette and Derry 2016; Des Roches et al. 2017). Indeed, in some cases intraspecific variation can have a greater influence than interspecific differences on overall community responses to environmental change (Crutsinger et al. 2006; Siefert and Ritchie 2016; Raffard et al. 2019).

Furthermore, varied responses set the stage for future evolution, as the cohort of individuals capable of reproducing following an anthropogenic stress event defines the evolutionary potential of the population that remains after the disturbance event (Medina et al. 2007; Bijlsma and Loeschcke 2012). To consider only "mean" responses to anthropogenic stressors is therefore to underappreciate the likely consequences of the disturbance; a lack of population-level impacts may be masking more subtle but important within-population changes. Conversely, consideration of intraspecific variation facilitates a more comprehensive understanding of the impacts of anthropogenic stressors on animals, the likely consequences for wider ecosystems, and the best management strategies to address these changes.

While phenotypic plasticity can play a role in the persistence of individuals under changing environmental conditions (Nicotra et al., 2010), the extent of phenotypic plasticity can be limited by ecological and evolutionary constraints (Valladares et al., 2007). The distribution of traits within a community is expected to reflect variation around a mean optimal phenotype for fitness and/or growth rate (Norberg et al., 2001; Enquist et al., 2015). This idea follows from a central paradigm in ecology (Whittaker, 1972) and evolutionary biology (Levins, 1968) where observed shifts in phenotypes, species' abundances, and composition across environmental gradients reflect the arrangement of phenotypes or species that maximizes fitness in different environments. Abiotic filters such as temperature or moisture that limit successful survival strategies promote convergence of traits around this optimal local phenotype (Keddy, 1992; Weiher and Keddy, 1999; Violle et al., 2012).

On the other hand, when competitive interactions are a dominant factor in species survival or environmental conditions are highly variable at a scale smaller than the study unit, there could be advantages to expressing more variable phenotypes that are not clumped at the optimal phenotype (Pacala and Tilman, 1994; Grime, 2006). However, tests of this theory have shown mixed results with some evidence for higher fitness (Lajoie and Vellend, 2018) or occurrence (Muscarella and Uriarte, 2016) when species are nearer the community trait mean while other cases showed no tendency for species in their preferred habitats to have trait values closer to the community mean (Mitchell et al., 2018). The importance of intraspecific variation in this dynamic is also unclear.

The Study of Intraspecific Variation

Two of the most studied aspects of intraspecific variation are variation in the behavior of individuals within a species, often called "**animal personality**", and variation in the diet of individuals within a species, often called "**individual specialization**".

Animal Personality

Personality in animals has been investigated across a variety of different scientific fields including agricultural science, animal behavior, anthropology, psychology, veterinary medicine, and zoology (Gosling 2001). Thus, the definition for animal personality may vary according to the context and scope of study. However, there is recent consensus in the literature for a broad definition that describes animal personality as individual differences in behavior that are consistent across time and ecological context (Wolf et al. 2012). Here, consistency refers to the repeatability of behavioral differences between individuals and not a trait that presents itself the same way in varying environments (Réale et al. 2007; Stamps and Groothuis 2010).

Animal personality traits are measurable and are described in over 100 species (Carere and Locurto 2011). Personality in animals has also been referred to as animal disposition, coping style, and temperament (Gosling 2001). There are also personality norms through the species, often found between genders (Gosling 2008). The diversity of animal personality can be compared in cross-species studies, demonstrating its pervasiveness in the evolutionary process of animals (Gosling 2001). Research on animal personality variation has been burgeoning since the mid 1990s (Kralj-Fišer and Schuett 2014). Recent studies have focused on its proximate causation and the ecological and evolutionary significance of personality in animals (Stamps and Groothuis 2010).

Example: The spider *Anelosimus studiosus* forms groups in which some females show an aggressive personality type and engage more in colony defense and prey capture, while others are docile and engage more in brood care. Groups containing both these two different personalities have better fitness than groups of only one personality type. This is because aggressive females are more efficient at foraging, web construction and defense, while docile females are better at raising the young. When groups contain a mix of both personalities, overall group performance is improved benefiting all group members (Grinsted and Bacon 2014). In the social spider *Stegodyphus dumicola* individuals differ in their boldness, with bolder individuals having a greater risk appetite. Boldness changes were found to relate to social interactions with nest mates, indicating that individual personality is more plastic in groups (Hunt et al. 2018).

Animal personality vs. human personality

The extent of personality phenomenon considered when examining animal personality is significantly reduced compared to those studied in humans. Concepts such as personal objects, identity, attitudes and life stories are not considered relevant in animals. Similarly, any approach that requires the subject to explain motives, beliefs or feelings is not applicable to the study of animal behavior (Gosling 2001).

The study of animal personality is largely based on the observation and investigation of behavioral traits. In an ecological context, traits or 'characters' are attributes of an organism that are shared by members of a species. Traits can be shared by all or only a portion of individuals in a population. For example, studies in animal personality often examine traits such as aggressiveness (antagonistic interactions with other individuals of the same species), boldness (reaction to risky situations), exploration (reaction to new situations), activity (movement in a familiar environment), and sociality (positive interactions with other individuals of the same species).

Quantifying Intraspecific Variation in Behavior: Repeatability

Repeatability refers to the fraction of variation in a population that is owed to differences between individuals. Repeatability estimates are one of the most widely used statistical tools that can quantify consistent individual differences in behavior (Biro et al. 2015). Formally,

$$r = \left(\frac{S_A^2}{S_A^2 + S^2} \right)$$

where, S_A^2 is variance among individuals and S^2 is the variance within individuals over time (Leclerc et al. 2016). In a meta-analysis of published, peer-reviewed repeatability estimates, reviewers found that, in general, approximately 35% of behavioral variation among individuals could be attributed to individual differences (Bell et al. 2009).

Evolutionary potential

The degree of variation in a population has been determined to influence the direction and outcome of natural selection. Most scientific research has focused on genetic and phenotypic variation or differences in resource use; however, variation in consistent behaviors (i.e. personality) also has important evolutionary consequences. For example, personality in animals can affect the way individuals interact with their environment and with each other which can affect the relative fitness of individuals (Biro and Stamps

2008). Therefore, personality can influence selection. Also, behavioral traits are more dynamic which may allow an animal to adapt more quickly which, in turn, can speed up the rate of evolution (Wolf and Weissing 2012).

Further, natural or artificial selection cannot act on personality unless there is a mechanism for its inheritance. In rhesus macaques (*Maccaca mulatta*), the personality traits of Meek, Bold, Aggressive, Passive, Loner and Nervous have heritability values of 0.14 to 0.35, thus indicated that there is some genetic basis to the expression of personality traits in animals. In apes, including humans, heritability estimates of personality dimensions range from 0.07 to 0.63 (Brent et al. 2014). In horses, heritability estimates range mostly between h2=0.15 and h2=0.40 for traits assessed in personality tests. Values at this level are considered as "promising" for artificial selection (Brent et al. 2014).

Personality in Practice *Chapter*13.1

Reaction norms help us study personality and plasticity

A potentially useful way to understand how individual variation interacts with the factors known to influence phenotypic traits is to view a phenotypically plastic trait using a reaction norm. A reaction norm is the set of phenotypes a genotype/individual could express across a set of environments (Via et al. 1995). The reaction norm has a long history for studying phenotypic variation (Stearns 1989; Pigliucci 2001). Using a reaction norm model (see below) we can study individual variation in a phenotypic trait in terms of individual deviation from the population mean, as well as individual variation from the mean population response to the environmental (individual phenotypic plasticity). A reaction norm approach can also allow insight into how and why individuals vary in different dimensions, both in their mean expression of a trait (reaction norm height) and the plasticity of the trait (reaction norm slope). The basic reaction norm to study how a trait (y) varies with some environmental factor (E) can be written as:

$$y_{ij} = \mu + \beta E_j + p_i + p_{Ei}E_j + \varepsilon_{ij}$$

where y_{ij} is the phenotype of individual i on occasion j. This equation contains two main effects, the fixed effects and the random effects, and the residual error effects. The fixed effects represent the population average response of the trait (y) to the change in the environment (E). The fixed effects include the variables μ, which is the population mean phenotype in the average environment, and β, which is the population mean slope of y on E. The random effects represent individual phenotypic differences from the population average height and slope. The random effects include the variables p_i, which is the permanent deviation of individual i from the mean population phenotype independent of E (**personality**: individual reaction norm height), and p_{Ei}, which is the deviation of individual i from the population average slope (**individual plasticity**). The best way to interpret this equation may be to visualize what each component means in graphical form (Figure 13.4). The reaction norm approach allows us to estimate the variance in a trait that is due to the effect of individual variation. We can also test for significant differences in the variance in height of the individual reaction norms (Vp) to see if individuals differ in their average phenotype, as well as test for differences in the variance of individual slopes of the reaction norms (VpE; Figure 13.5).

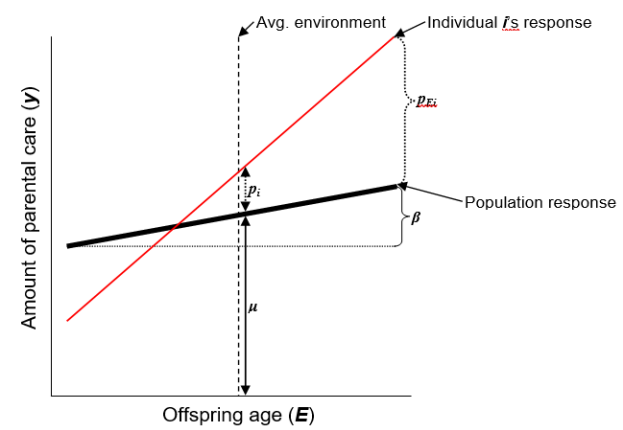


Figure 13.4: This diagram represents the basic reaction norm model, where the phenotype *y* is the amount of parental care and the environment *E* is the age of offspring. The variable μ represents the population mean phenotype in the average environment, and β is the population mean slope. The random effects are represented by *pi*, which is the permanent deviation of individual *i* from the mean population phenotype (**personality**: individual reaction norm height), and *pEi*, which is the deviation of individual *i* from the population average slope (individual **plasticity**).

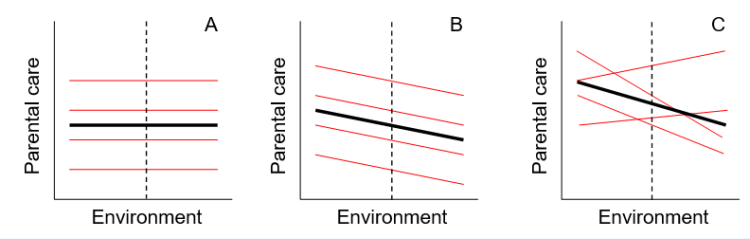


Figure 13.5: These diagrams represent examples of reaction norms with different degrees of variation. The thick black line is the mean population response to the environment, and each thin red line represents an individual's phenotype across the environment. The diagrams show that: **(A)** there is individual variation in the phenotype (personality: heights of the red lines), but that there is no phenotypic plasticity, **(B)** there is individual variation in the phenotype (personality: heights of the red lines), there is population-level phenotypic plasticity (slopes of the red lines are non-zero), but individuals do not differ in their response to the environment (slopes of the red lines are equal), and **(C)** there is individual variation in the phenotype (personality: heights of the red lines), there is population-level phenotypic plasticity (slopes of the red lines are non-zero), and individuals differ in their response to the environment (individual plasticity: slopes of the red lines vary).

Individual Specialization in Foraging and Diet

Individuals can vary in the quantity of resources they consume, the type of resources they consume, and how they obtain these resources (i.e., in their foraging behavior). This variation in diet and foraging behavior can be linked to animal personality. For example, more aggressive individuals are likely to benefit from social dominance that allows them access to higher quality resources than subordinate individuals (Toscano et al. 2016).

Individual specialization is specifically used to describe variation in diet among individuals that is not driven by *a priori* factors like morphology, sex, or age. In the formula below, diet is driven by variation due to sex, age, morphology, and random differences among individuals; these random differences represent intraspecific variation in diet (Bolnick et al. 2003).

diet = sex + age + morphology + random differences

Measuring Intraspecific Variation

Intraspecific variation in diet and foraging is studied using traditional tools (e.g., observation, gut content analysis) as well as more modern tools such as stable isotope analysis and animal tagging. These tools have considerable advantages in studying animal foraging behavior (tagging) and diet (stable isotope analysis).

Tagging data is particularly useful because it provides high-frequency, continuous data that allows researchers to determine multiple ways in which animals vary in their foraging (e.g., foraging distance, foraging location, diving depth) and how they alter this behavior when conditions change. In Figure 13.6, for example, individual great black-backed gulls (*Larus marinus*) vary in where they forage and in how they shift their foraging locations when food availability declines.

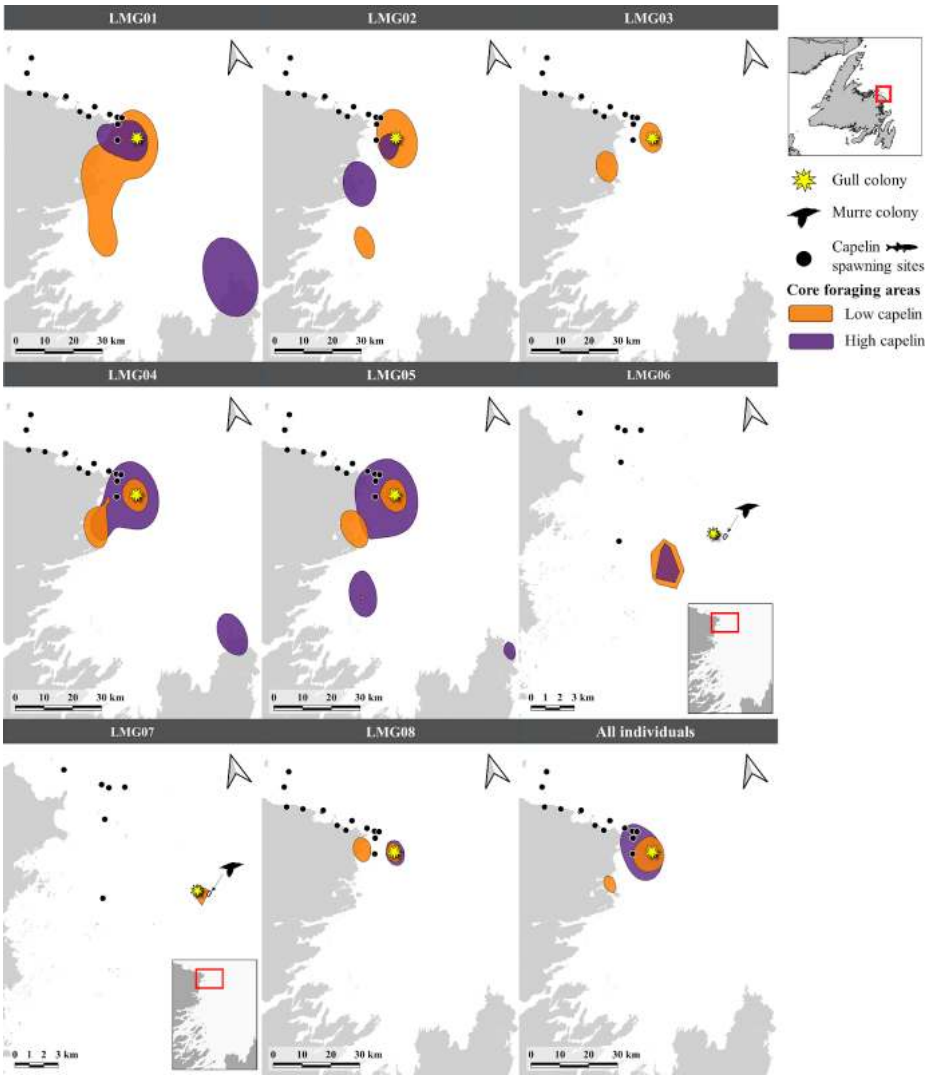


Figure 13.6: Differences in space use of individual great black-backed gulls (*Larus marinus*) foraging on capelin (*Mallotus villosus)*, a small schooling fish species, in Newfoundland, Canada. Individuals vary not only in the average size and location of their foraging areas, but also in how much they shift these areas from high food availability (High capelin; purple) to low food availability (Low capeline; orange). Murre (*Uria aalge*) are another species of seabird that breed in this region and consume capelin.

The concept of intraspecific variation in diet is closely related to the concept of **generalist** versus **specialist** populations. In a **specialist population**, all individuals use similar resources and a narrow range of resources. **Generalist populations** use a wide range of resources, but this can be due to 1) individuals in the population all using a wide range of resources (true generalists) or 2) individuals in the population specializing on different resources, so that the overall population niche is wide but individual niches are not (generalist-specialists). In Figure 13.2, for example, the generalist population is made up of specialists. More information on these concepts can be found in the chapter on animal behavior, and specifically in the sections on Animal Foraging and Animal Movement.

Individual variation in diet is often studied using stable isotope analysis. Stable isotope analysis of diet is based on the idea that "you are what you eat". In other words, your elemental composition is determined by that of what you consume. All biologically active elements exist in a number of different isotopic forms, of which two or more are stable. For example, most carbon is present as 12C, with approximately 1% being 13C. The ratio of the two isotopes may be altered by biological and geophysical processes,

and these differences can be used in a number of ways by ecologists. The main elements used in diet studies are carbon and nitrogen (Michener and Lajtha 2007).

Carbon-13

Carbon isotopes aid us in determining the primary production source responsible for the energy flow in an ecosystem. The transfer of 13C through trophic levels remains relatively the same, except for a small increase (an enrichment < 1 ‰). Large differences of δ13C between animals indicate that they have different food sources or that their food webs are based on different primary producers (i.e. different species of phytoplankton, marsh grasses.) Because δ13C indicates the original source of primary producers, the isotopes can also help us determine shifts in diets, both short term, long term or permanent. These shifts may even correlate to seasonal changes, reflecting phytoplankton abundance (Michener and Kaufman 2007). Scientists have found that there can be wide ranges of δ13C values in phytoplankton populations over a geographic region. While it is not quite certain as to why this may be, there are several hypotheses for this occurrence. These include isotopes within dissolved inorganic carbon pools (DIC) may vary with temperature and location and that growth rates of phytoplankton may affect their uptake of the isotopes.

Nitrogen-15

Nitrogen isotopes indicate the trophic level position of organisms (reflective of the time the tissue samples were taken). There is a larger enrichment component with δ15N because its retention is higher than that of 14N. This can be seen by analyzing the waste of organisms (Michener and Kaufman 2007). Cattle urine has shown that there is a depletion of 15N relative to the diet (Kelly et al. 2002). As organisms eat each other, the 15N isotopes are transferred to the predators. Thus, organisms higher in the trophic pyramid have accumulated higher levels of 15N (and higher δ15N values) relative to their prey and others before them in the food web. Numerous studies on marine ecosystems have shown that on average there is a 3.2‰ enrichment of 15N vs. diet between different trophic level species in ecosystems (Michener and Kaufman 2007). In the Baltic sea, Hansson et al. (1997) found that when analyzing a variety of creatures (such as particulate organic matter (phytoplankton), zooplankton, mysids, sprat, smelt and herring,) there was an apparent fractionation of 2.4‰ between consumers and their apparent prey (Doucett et al. 2007).

In addition to comparing signatures across individuals, stable isotopes can be used to examine phenotypic plasticity because different tissue types (fur, blood, muscle) have different turnover rates and therefore reflect the diet of individuals across different timescales (Figure 13.7). Therefore, if multiple tissue types are collected from an individual, the diet of that individual can be examined over multiple temporal scales to determine how much variation there is within the individual's diet (i.e., how flexible their diet is).

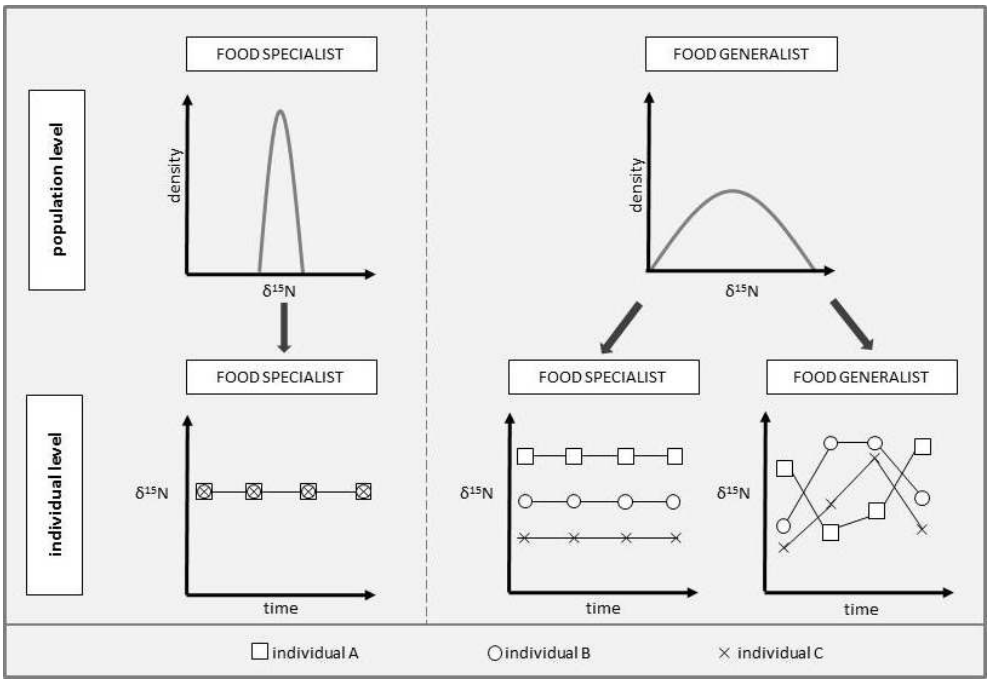


Figure 13.7: Conceptual diagram of how individuals can contribute to the population's dietary niche. Specialized populations consist of specialized individuals which all consume certain resources (left). Therefore, their total dietary niche represents a small dietary variation within and between individuals. In contrast, generalistic populations can consist either of specialized or generalistic individuals (right). In this case, specialized individuals show small dietary variation within individuals, but a large dietary variation between individuals leads to a broad overall resource spectrum and dietary variation at the population level. If individuals of a generalistic population forage generalistic then those are characterized by a large within-individual dietary variation. Taken from Scholz et al. 2020.

Quantifying Intraspecific Variation

Whether using isotope data or another continuous indicator of resources use (e.g., seed size; Figures 13.2 and 13.8), intraspecific variation can be quantified by comparing the average width of the individual niche (WIC - within individual component of niche variation) to the total niche width (TNW). The total niche width is equal to the WIC plus the BIC, or the between-individual component of niche variation (Bolnick et al. 2003). When BIC/TNW is relatively high, there is high intraspecific variation (i.e., individuals have consistent dietary preferences but these preferences vary across individuals) and the population is a specialist-generalist population (Figure 13.8A). When WIC/TNW is relatively high, all individuals show considerable variation in diet but have highly overlapping niches and the population is a true population of generalists (Figure 13.8B).

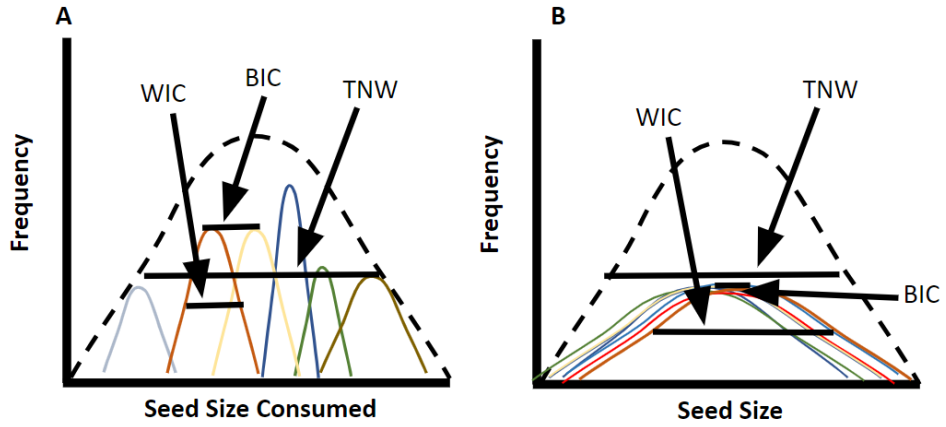


Figure 13.8: An example of intraspecific variation in a species of finch consuming seeds. Figure 13.8A shows a generalist population of specialists. While the range of seed sizes consumed by the population is large, individuals within the population each only consume a small range of seed sizes. Therefore, the within-individual component of variation (WIC) is a small proportion of the total niche width (TNW) and intraspecific variation is high. Figure 13.8B shows a generalist population of generalists. Since all individuals within this population consume a wide range of seed sizes, the WIC is high and intraspecific variation is low.

Case Study *Chapter*13.1

Intraspecific Variation in the Diet of Red Foxes

Some carnivores are known to survive well in urban habitats, yet the underlying behavioral tactics are poorly understood. One likely explanation for the success in urban habitats might be that carnivores are generalist consumers. However, urban populations of carnivores could as well consist of specialist feeders.

Scholz et al. (2020) compared the isotopic specialization of red foxes in urban and rural environments, using both a population and an individual level perspective. They measured stable isotope ratios in increments of red fox whiskers and potential food sources. Their results reveal that red foxes have a broad isotopic dietary niche and a large variation in resource use (Figure 13.9).

Despite this large variation, they found significant differences between the variance of the urban and rural population for $\delta^{13}C$ as well as $\delta^{15}N$ values, suggesting a habitat-specific foraging behavior. Although urban regions have more heterogeneous land cover than rural regions, the dietary range of urban foxes was smaller compared with that of rural conspecifics. Moreover, the higher $\delta^{13}C$ values and lower $\delta^{15}N$ values of urban foxes suggest a relatively high input of anthropogenic food sources.

The diet of most individuals remained largely constant over a longer period. The low intraindividual variability of urban and rural red foxes suggests a relatively constant proportion of food items consumed by individuals. Urban and rural foxes utilized a small proportion of the potentially available isotopic dietary niche as indicated by the low within-individual variation compared to the between-individual variation. Scholz et al. (2020) conclude that generalist fox populations consist of individual food specialists in urban and rural populations.

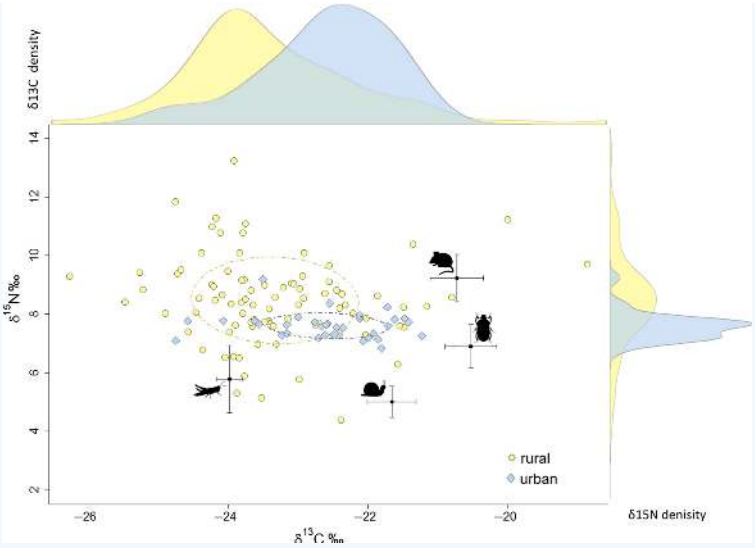


Figure 13.9: Isospace and density plot for raw δ13C and δ15N values of urban (blue diamonds) and rural (yellow circles) red foxes whisker samples (*n* = 119) from Berlin and Brandenburg, Germany. Dashed ellipses represent SEAc of the urban (blue) and rural (yellow) fox population. Black dots show trophic corrected mean (±SE bars) δ13C and δ15N values for the four prey taxa including (1) grasshopper, (2) land slug, land snail, earthworm (pooled together), (3) dor beetle, and (4) house mouse. Taken from Scholz et al. 2020.

Summary

While ecological studies sometimes focus on variation among species (interspecific variation) there is often substantial variation in the traits and behaviors of individuals within a species (intraspecific variation). Individuals might vary in their mean phenotype and in how much their phenotype responds to changes in their environment (phenotypic plasticity). Two key fields of research into intraspecific variation include animal personality, variation in the behavior of individuals within a species, and individual specialization, variation in the diet of individuals within a species.

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- **Phenotypic plasticity by Wikipedia, the free encyclopedia**
- **Personality in Animal by Wikipedia, the free encyclopedia**
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CHAPTER OVERVIEW

Chapter 14: Introduction to Community Ecology

Learning Objectives

- Develop an appreciation of the interconnected nature of ecological communities
- Organize species interactions based on their impacts on the species involved
- Understand some of the factors that structure ecological communities



Scientist Spotlight - Anurag Agrawal

Introduction to Species Interactions

Populations rarely, if ever, live in isolation from populations of other species. All populations occupying the same habitat form a **community** (populations of multiple species inhabiting a specific area at the same time). The number of species occupying the same habitat and their relative abundance is known as species diversity. Areas with low diversity, such as the glaciers of Antarctica, still contain a wide variety of living things, whereas the diversity of tropical rainforests is so great that it cannot be counted. Ecology is studied at the community level to understand how species interact with each other and compete for the same resources.

The interactions among populations of different species play a major role in regulating population growth and abundance. A **species interaction** is the effect that a pair of organisms living together in a community have on each other. Interactions range from mutualism, which benefits both species involved, to competition, which harms both species involved (Wootton and Emmerson 2005). Interactions can be indirect, through intermediaries such as shared resources or common enemies. All of these interactions can be organized by the effects the species have on each other (Figure 1).

Species interactions may be short-term, like pollination and predation, or long-term; both often strongly influence the evolution of the species involved. Short-term interactions are short-lived in terms of the duration of a single interaction: a predator kills and eats a prey; a pollinator transfers pollen from one flower to another; but they are extremely durable in terms of their influence on the evolution of both partners. As a result, the partners coevolve (Bengtson 2002, Lunau 2004).

Interaction	Species 1	Species 2	Example
Competition	-	-	Blue mussels (Species 1) competing with barnacles (Species 2) for space in the intertidal zone
Mutualism	+	+	Zooxanthellae (Species 1) providing coral (Species 2) with photosynthate and gaining nutrients from the coral
Antagonistic (Predation, Parasitism, Herbivory)	-	+	An antelope (Species 1) killed and consumed by a lion (Species 2)
Amensalism	-	0	Insects (Species 1) crushed by a walking elephant (Species 2)
Commensalism	+	0	Remora (Species 1) catching a ride on a large shark (Species 2)
Neutralism	0	0	Two species without niche overlap sharing a habitat

Figure $Chapter 14.1$: Summary of species interactions, showing how each species is impacted by the interaction. Produced by N. Gownaris.

Antagonistic Interactions

Predation

In predation, one organism, the predator, kills and eats another organism, its prey. Predators are adapted and often highly specialized for hunting, with acute senses such as vision, hearing, or smell. Many predatory animals, both vertebrate and invertebrate, have sharp claws or jaws to grip, kill, and cut up their prey. Other adaptations include stealth and aggressive mimicry that improve hunting efficiency. Predation has a powerful selective effect on prey, causing them to develop antipredator adaptations such as warning coloration, alarm calls and other signals, camouflage and defensive spines and chemicals (Royal Saskatchewan Museum 2012, Bar-Yam 2018, Vermeij 1993). Predation has been a major driver of evolution since at least the Cambrian period (Bengston 2002). Predators control the population dynamics of their prey and vice versa and ecologists model these dynamics using coupled equations known as the Lotka-Volterra predator-prey model. These models will be covered in more detail in the chapter on Antagonistic Interactions.



Figure *Chapter*14.1: Predation is a short-term interaction in which the predator kills and eats its prey. An osprey (a) uses exceptional eyesight as well as sharp talons and beak to catch prey. The tropical walking stick (b) and the chameleon (c) use body shape and/or coloration to prevent detection by predators. (credit b: modification of work by Linda Tanner; credit c: modification of work by Frank Vassen)

Parasitism

Parasitism is a relationship between species, where one organism, the parasite, lives on or in another organism, the host, causing it some harm, and is adapted structurally to this way of life (Poulin 2007). The parasite either feeds on the host, or, in the case of intestinal parasites, consumes some of its food (Martin and Schwab 2013). Not all parasites kill their hosts, but some do. **Parasitoids** are parasites that lay their eggs within a host. The larvae of parasitoids eventually hatch out of the host's body, killing the host.

Competition

Competition can be defined as an interaction between organisms or species, in which the fitness of one is lowered by the presence of another. Competition is often for a resource such as food, water, or territory in limited supply, or for access to females for reproduction (Begon et al. 1996). Competition among members of the same species is known as **intraspecific competition**, while competition between individuals of different species is known as **interspecific competition**.

According to the **competitive exclusion principle**, no two species with the same ecological niche can coexist, and the species less suited to compete for resources should either adapt or die out (Hardin 1960; Pocheville 2015). Competition within and between species for resources plays a critical role in natural selection (Sahney et al. 2010). Ecologists model competition using the Lotka-Volterra competition model, and use this model to predict the conditions under which two species will coexist or one species outcompetes the other. These models will be covered in more detail in the chapter on Competition.



Figure *Chapter*14.1: The black walnut secretes a chemical from its roots that harms neighboring plants, an example of competitive antagonism.

Beneficial Interactions

Mutualism

A mutualism is an interaction between two or more species, where both species derive a mutual benefit. One or both species involved in the interaction may be obligate, meaning they cannot survive in the short or long term without the other species (**obligate mutualism**). In other cases, though both species benefit, they may not need the mutualistic interaction to survive (**facultative mutualism**). Though mutualism has historically received less attention than other interactions such as predation (Begon et al. 1996), it is an ecologically important interaction.



Figure *Chapter*14.1: (a) Termites form a mutualistic relationship with symbiotic protozoa in their guts, which allow both organisms to obtain energy from the cellulose the termite consumes. (b) Lichen is a fungus that has symbiotic photosynthetic algae living inside its cells. (credit a: modification of work by Scott Bauer, USDA; credit b: modification of work by Cory Zanker)

Pollination and Seed Dispersal

In pollination, pollinators including insects (**entomophily**), some birds (**ornithophily**), and some bats, transfer pollen from a male flower part to a female flower part, enabling fertilization, in return for a reward of pollen or nectar (CropsReview.Com 2015). Plants and pollinators are often coevolved (Ehrlich and Raven 1964; Pollan 2001; Lunau 2004). Insect-pollinated flowers have bright colors, patterns, scent, nectar, and sticky pollen to attract insects, guide them to pick up and deposit pollen, and reward pollinators. Conversely, pollinator insects like bees are adapted to detect flowers by color, pattern, and scent, to collect pollen (such as with bristles shaped to form pollen baskets on their hind legs), and nectar.



Figure $Chapter 14.1$: Hummingbird hawkmoth drinking from Dianthus.

Seed dispersal is the movement, spread or transport of seeds. Plants have limited mobility and rely upon a variety of dispersal vectors to transport their propagules, including both abiotic vectors such as the wind and living (biotic) vectors like birds (Lim ad Burns 2021) patterns of seed dispersal are determined in large part by the dispersal mechanism and this has important implications for the demographic and genetic structure of plant populations, as well as migration patterns and species interactions. There are five main modes of seed dispersal: gravity, wind, ballistic, water, and animals.

Other Types of Interactions

Amensalism

Amensalism (a term introduced by Haskell; Toepfer) is an interaction where an organism inflicts harm to another organism without any costs or benefits received by itself (Willey et al. 2013). Amensalism describes the adverse effect that one organism has on another organism. A classic example of amensalism is where sheep or cattle trample grass. Whilst the presence of the grass causes negligible detrimental effects to the animal's hoof, the grass suffers from being crushed.

Amensalism is often used to describe strongly asymmetrical competitive interactions, such as has been observed between the Spanish ibex and weevils of the genus Timarcha which feed upon the same type of shrub. Whilst the presence of the weevil has almost no influence on food availability, the presence of ibex has an enormous detrimental effect on weevil numbers, as they consume significant quantities of plant matter and incidentally ingest the weevils upon it (Gómez and González-Megías 2002).

Commensalism

Commensalism benefits one organism while the other organism neither benefits nor is harmed. It often occurs when one organism benefits from an interaction with another organism that is not affected. A good example is a remora living with a manatee. Remoras feed on the manatee's feces. The manatee is not affected by this interaction, as the remora does not deplete the manatee's resources (Williams and Williams 2003).



Figure *Chapter*14.1:

The southern masked-weaver bird is starting to make a nest in a tree in Zambezi Valley, Zambia. This is an example of a commensal relationship, in which one species (the bird) benefits, while the other (the tree) neither benefits nor is harmed. (credit: "Hanay"/Wikimedia Commons)

Case Study: Non-Trophic Interactions and Foundation Species *Chapter*14.1

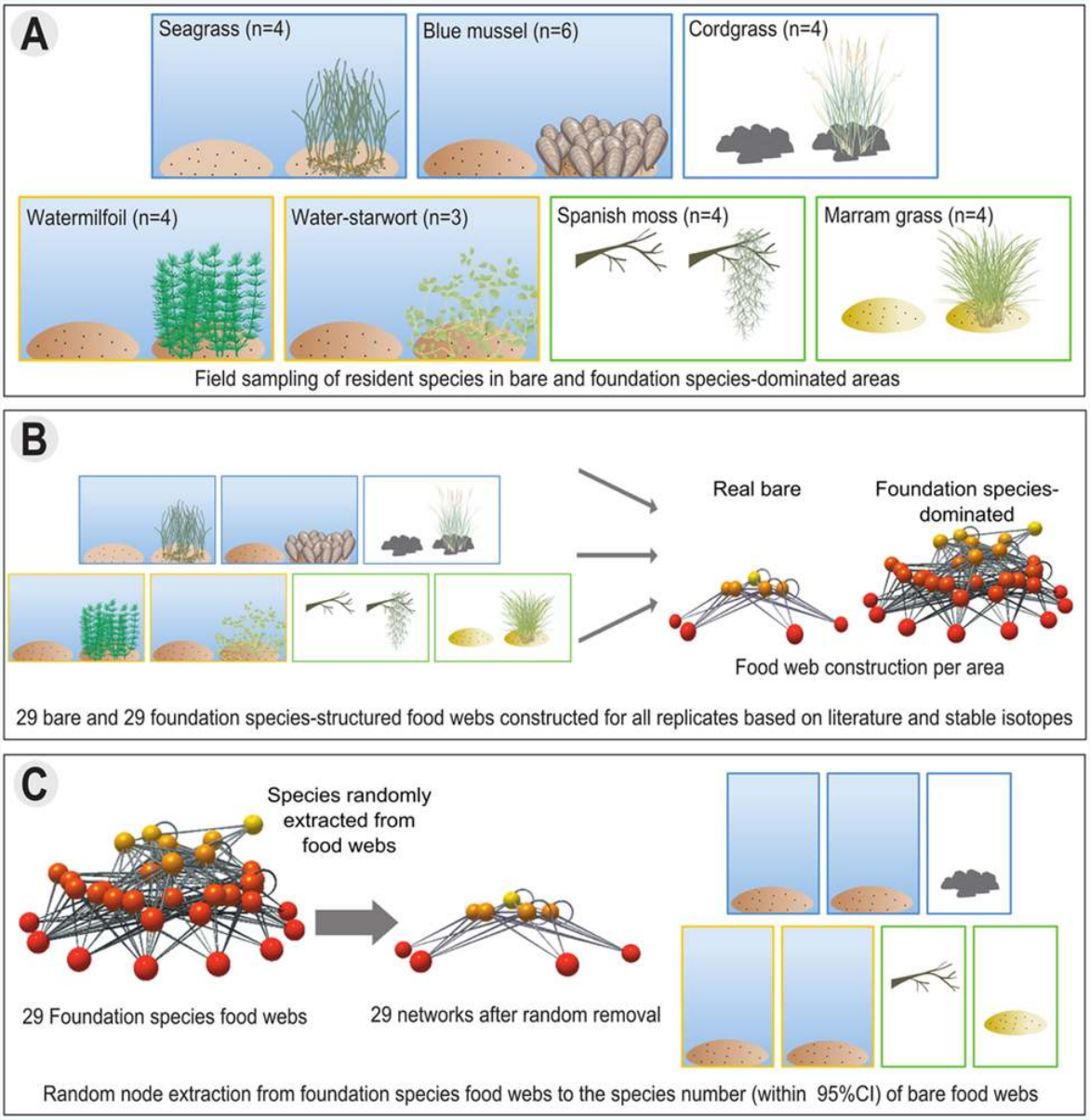


Figure 9: Foundational species increase food web complexity by facilitating species higher in the food chain. (A) Seven ecosystems with foundation species were sampled: coastal (seagrass, blue mussel, cordgrass), freshwater (watermilfoil, water-starwort) and terrestrial (Spanish moss, marram grass). (B) Food webs were constructed for both bare and foundation species-dominated replicate areas. (C) From each foundation species structured-food web, nodes (species) were randomly removed until the species number matched the species number of the bare food webs.

Although we often focus on trophic (food-related) interactions among species, there is growing evidence that non-trophic interactions can indirectly affect food web topology and trophic dynamics by affecting the species in the network and the strength of trophic links (Sanders et al. 2014; Kefi et al. 2015; van der Zee et al. 2016). Some examples of non-trophic interactions are habitat modification and competition for space.

Foundation species are spatially dominant habitat-structuring organisms (Dayton 1972; Governar 2010; Angelini et al. 2011). Although foundation species are part of the food web like any other species (e.g. as prey or predator), numerous studies have shown that they strongly facilitate the associated community by creating new habitat and alleviating physical stress (Bertness et al. 1999; Jones et al. 2010; Reid and Lortie 2012; Angelini and Silliman 2014; Kefi et al. 2015; van der Zee EM et al. 2015;

van der Zee et al. 2016; Filazzola et al. 2017). This form of non-trophic facilitation by foundation species has been found to occur across a wide range of ecosystems and environmental conditions (Bertness and Callaway 1994; Bruno et al. 2003). In harsh coastal zones, corals, kelps, mussels, oysters, seagrasses, mangroves, and salt marsh plants facilitate organisms by attenuating currents and waves, providing aboveground structure for shelter and attachment, concentrating nutrients, and/or reducing desiccation stress during low tide exposure (Bertness and Callaway 1992; Angelini et al. 2011). In more benign systems, foundation species such as the trees in a forest, shrubs and grasses in savannahs, and macrophytes in freshwater systems, have also been found to play a major habitat-structuring role (Jeppesen et al. 1992; Bertness and Callaway 1994; Bruno et al. 2003; Ellison et al. 2005). Ultimately, all foundation species increase habitat complexity and availability, thereby partitioning and enhancing the niche space available to other species (Bruno et al. 2003; Bulleri et al. 2016; Borst et al. 2018).

Borst et al. (2018) tested the general hypothesis that foundation species modify food webs by enhancing their size as indicated by species number, and their complexity as indicated by link density, via facilitation of species, regardless of ecosystem type (Figure 6). Additionally, Borst et al. 2018 examined whether any change in food web properties caused by foundation species occurs via random facilitation of species throughout the entire food web or via targeted facilitation of specific species that belong to certain trophic levels or functional groups. They found that species at the base of the food web are less strongly facilitated, and carnivores are more strongly facilitated, in foundation species' food webs than predicted based on random facilitation, resulting in a higher mean trophic level and a longer average chain length. This indicates foundation species strongly enhance food web complexity through non-trophic facilitation of species across the entire trophic network (Borst et al. 2018).

Overview of Community Structure and Dynamics

Communities are complex entities that can be characterized by their structure (the types and numbers of species present) and dynamics (how communities change over time). Understanding community structure and dynamics enables community ecologists to manage ecosystems more effectively.

Foundation Species

Foundation species are considered the “base” or “bedrock” of a community, having the greatest influence on its overall structure. They are usually the primary producers: organisms that bring most of the energy into the community. Kelp, brown algae, is a foundation species, forming the basis of the kelp forests off the coast of California.

Foundation species may physically modify the environment to produce and maintain habitats that benefit the other organisms that use them. An example is the photosynthetic corals of the coral reef. Corals themselves are not photosynthetic, but harbor symbionts within their body tissues (dinoflagellates called zooxanthellae) that perform photosynthesis; this is another example of a mutualism. The exoskeletons of living and dead coral make up most of the reef structure, which protects many other species from waves and ocean currents.



Figure $Chapter 14.1$: Coral is the foundation species of coral reef ecosystems. (credit: Jim E. Maragos, USFWS)

Biodiversity, Species Richness, and Relative Species Abundance

Biodiversity describes a community's biological complexity: it is measured in many ways, the simplest of which is by the number of different species (species richness) in a particular area and their relative abundance. Species richness varies across the globe. One factor in determining species richness is latitude, with the greatest species richness occurring in ecosystems near the equator, which often have warmer temperatures, large amounts of rainfall, and low seasonality. The lowest species richness occurs near the poles, which are much colder, drier, and thus less conducive to life in Geologic time (time since glaciations). The predictability of climate or productivity is also an important factor. Other factors influence species richness as well. For example, the study of island biogeography attempts to explain the relatively high species richness found in certain isolated island chains, including the Galápagos Islands that inspired the young Darwin. Foundation species often have the highest relative abundance or biomass of all species in a community.

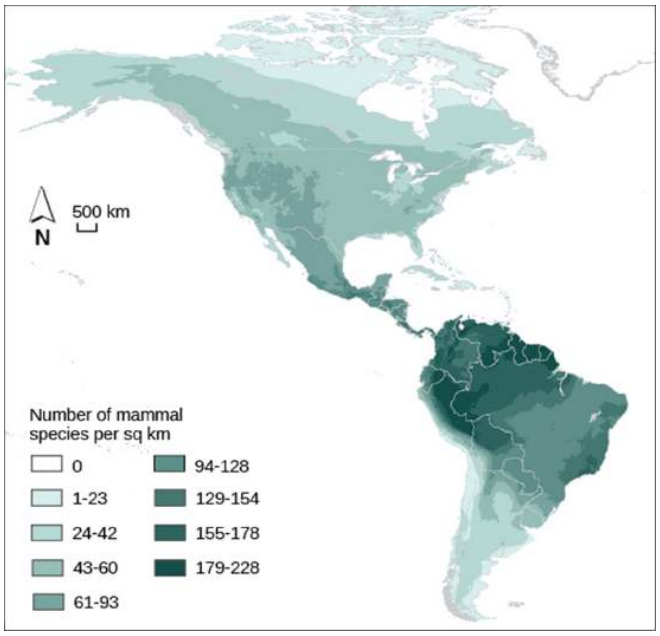


Figure *Chapter*14.1: The greatest species richness for mammals in North and South America is associated with the equatorial latitudes. (credit: modification of work by NASA, CIESIN, Columbia University)

Keystone Species

A keystone species is one whose presence is key to maintaining biodiversity within an ecosystem and to upholding an ecological community's structure. The intertidal sea star, *Pisaster ochraceus*, of the northwestern United States is a keystone species. Studies have shown that when this organism is removed from communities, populations of their natural prey (mussels) increase, completely altering the species composition and reducing biodiversity. Another keystone species is the banded tetra, a fish in tropical streams, which supplies nearly all of the phosphorus, a necessary inorganic nutrient, to the rest of the community. If these fish were to become extinct, the community would be greatly affected.



Figure $Chapter 14.1$: The *Pisaster ochraceus* sea star is a keystone species. (credit: Jerry Kirkhart)

Community Dynamics

Community dynamics are the changes in community structure and composition over time. Sometimes these changes are induced by environmental disturbances such as volcanoes, earthquakes, storms, fires, and climate change. Communities with a stable structure are said to be at equilibrium. Following a disturbance, the community may or may not return to the equilibrium state.

Succession describes the sequential appearance and disappearance of species in a community over time. In primary succession, newly exposed or newly formed land is colonized by living things; in secondary succession, part of an ecosystem is disturbed and remnants of the previous community remain.



Figure $Chapter 14.1$: During primary succession in lava on Maui, Hawaii, succulent plants are the pioneer species. (credit: Forest and Kim Starr)

Everyday Connection: Invasive Species $Chapter 14.1$

Invasive species are non-native organisms that, when introduced to an area out of their native range, threaten the ecosystem balance of that habitat. Many such species exist in the United States, as shown in Figure 14 below. Whether enjoying a forest hike, taking a summer boat trip, or simply walking down an urban street, you have likely encountered an invasive species.

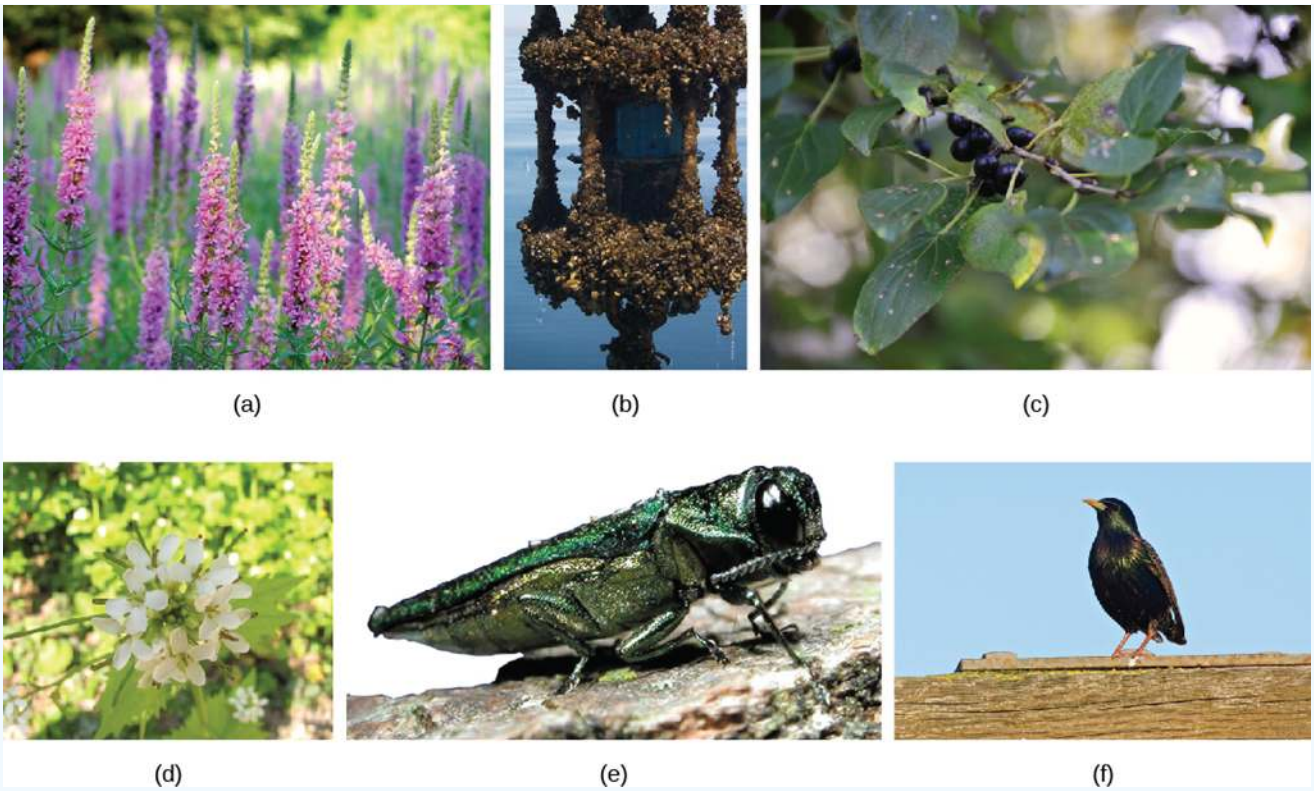


Figure 14: In the United States, invasive species like (a) purple loosestrife (*Lythrum salicaria*) and the (b) zebra mussel (*Dreissena polymorpha*) threaten certain aquatic ecosystems. Some forests are threatened by the spread of (c) common buckthorn (*Rhamnus cathartica*), (d) garlic mustard (*Alliaria petiolata*), and (e) the emerald ash borer (*Agrilus planipennis*). The (f) European starling (*Sturnus vulgaris*) may compete with native bird species for nest holes. (credit a: modification of work by Liz West; credit b: modification of work by M. McCormick, NOAA; credit c: modification of work by E. Dronkert; credit d: modification of work by Dan Davison; credit e: modification of work by USDA; credit f: modification of work by Don DeBold)

One of the many recent proliferations of an invasive species concerns the growth of Asian carp populations. Asian carp were introduced to the United States in the 1970s by fisheries and sewage treatment facilities that used the fish's excellent filter feeding capabilities to clean their ponds of excess plankton. Some of the fish escaped, however, and by the 1980s they had colonized many waterways of the Mississippi River basin, including the Illinois and Missouri Rivers.

Voracious eaters and rapid reproducers, Asian carp may outcompete native species for food, potentially leading to their extinction. For example, black carp are voracious eaters of native mussels and snails, limiting this food source for native fish species. Silver carp eat plankton that native mussels and snails feed on, reducing this food source by a different alteration of the food web. In some areas of the Mississippi River, Asian carp species have become the most predominant, effectively outcompeting native fishes for habitat. In some parts of the Illinois River, Asian carp constitute 95 percent of the community's biomass. Although edible, the fish is bony and not a desired food in the United States. Moreover, their presence threatens the native fish and fisheries of the Great Lakes, which are important to local economies and recreational anglers. Asian carp have even injured humans. The fish, frightened by the sound of approaching motorboats, thrust themselves into the air, often landing in the boat or directly hitting the boaters.

The Great Lakes and their prized salmon and lake trout fisheries are also being threatened by these invasive fish. Asian carp have already colonized rivers and canals that lead into Lake Michigan. One infested waterway of particular importance is the Chicago Sanitary and Ship Channel, the major supply waterway linking the Great Lakes to the Mississippi River. To prevent the Asian carp from leaving the canal, a series of electric barriers have been successfully used to discourage their migration; however, the threat is significant enough that several states and Canada have sued to have the Chicago channel permanently cut off from Lake Michigan. Local and national politicians have weighed in on how to solve the problem, but no one knows

whether the Asian carp will ultimately be considered a nuisance, like other invasive species such as the water hyacinth and zebra mussel, or whether it will be the destroyer of the largest freshwater fishery of the world.

The issues associated with Asian carp show how population and community ecology, fisheries management, and politics intersect on issues of vital importance to the human food supply and economy. Socio-political issues like this make extensive use of the sciences of population ecology (the study of members of a particular species occupying a particular area known as a habitat) and community ecology (the study of the interaction of all species within a habitat).

Summary

Populations of species do not exist in isolation – they exist in the context of coevolved ecological communities. Species interactions can harm both species involved (competition), benefit both involved (mutualism), or benefit one and harm the other (Predation, Parasitism, Herbivory). These interactions play a key role in evolution (e.g., prey evolve to avoid detection by predators) and in structuring ecological communities (e.g., loss of top predators can lead to drastic reductions in biodiversity). While some of these interactions involved trophic relationships, others, such as habitat-formation by foundation species, do not.

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Scientist Spotlight - Anurag Agrawal

During summer 2021, social media users may have noticed a brief spotlight shone on the invasive spotted lanternfly. This beautiful bug feeds on a wide array of lumber/silviculturally valuable trees, and officials have encouraged people to squash them on site. There may be ecological and evolutionary history explaining the spread of the spotted lanternfly in the United States. The story of the viburnum leaf beetle, revealed by ecologist Anurag Agrawal, may shed some light on this phenomenon.

The invasive viburnum leaf beetle has wreaked havoc on species of *Viburnum* shrub in the Northeastern United States by eating their leaves and laying eggs on their twigs. However, this antagonistic relationship did not always mean decimation for species of *Viburnum* shrub. Some *Viburnum* species share evolutionary history with the beetle, and this translates into an astonishing mechanism of plant defense. Anurag Agrawal is an ecologist at Cornell University studying the ecology and evolution of plant-insect interactions. His lab discovered the aforementioned evolutionary defense mechanism- old-world *Viburnum* shrubs crushing beetle eggs. Insect herbivory incites something called an "evolutionary arms race", where the plant evolves defense mechanisms to avoid predation, the insect evolves in response to evolutionary pressure imposed by that defense mechanism, and the race goes back and forth as each party tries to 'out-evolve' the other. This is also called the "red queen hypothesis." In contrast, North American *Viburnum* species did not coevolve with the beetle. While they mount the same defense response as their old-world cousins, it is distinctly weaker. This "convergent continental difference" in defense response is one of many plant-insect interactions Agrawal has studied in relation to evolution.

Dr. Agrawal shared that "In general Asian-Americans are well-represented in STEM, but less so in ecology and evolution." He rarely thinks of himself as under-represented, but "Recognizing this has occasionally brought out an important insight."





"Viburnum leaf beetle" by Eltore Balocchi is licensed under CC BY 2.0. "Anurag Agrawal with Asclepias welshii" by Anuragagrawal99 is licensed under CC BY-SA 4.0.

Sources

Spotlight inspiration from Project Biodiversify

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CHAPTER OVERVIEW

Chapter 15: Competition

Learning Objectives

- Discuss the many levels of interaction such as predation, herbivory, competition, and symbiosis between living organisms within a population, within a community, and within an ecosystem.



15.1: Introduction and Types of Competition
15.2: Intraspecific (Single Species) Competition
15.3: Interspecific (Two Species) Competition
15.4: Ecological Consequences of Competition
15.5: Quantifying Competition Using the Lotka-Volterra Model
15.6: References and Attributions

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15.1: Introduction and Types of Competition

Introduction to Competition

Competition is an interaction between organisms or species in which both require a resource that is in limited supply (such as food, water, or territory). Competition lowers the fitness of both organisms involved since the presence of one of the organisms always reduces the amount of the resources available to the other.



Figure 15.1.1: *Sea anemones compete for the territory in tide pools*

In the study of community ecology, competition within and between members of a species is an important biological interaction. Competition is one of many interacting biotic and abiotic factors that affect community structure, species diversity, and population dynamics (shifts in a population over time). Competition within and between species for resources is important in natural selection.

There are three major mechanisms of competition: interference, exploitation, and apparent competition (in order from most direct to least direct). Interference and exploitation competition can be classed as "real" forms of competition, while apparent competition is not, as organisms do not share a resource, but instead share a predator. Competition among members of the same species is known as intraspecific competition, while competition between individuals of different species is known as interspecific competition. Diffuse competition refers to the summed effects of all competitors.

Studies show that intraspecific competition can regulate population dynamics (changes in population size over time). This occurs because individuals become crowded as a population grows. Since individuals within a population require the same resources, crowding causes resources to become more limited. Some individuals (typically small juveniles) eventually do not acquire enough resources and die or do not reproduce. This reduces population size and slows population growth. The logistic growth model, which includes a term for the species' carrying capacity, is a model of intraspecific competition.

Species also interact with other species that require the same resources. Consequently, interspecific competition can alter the sizes of many species' populations at the same time. Experiments demonstrate that when species compete for a limited resource, one species eventually drives the populations of other species extinct. According to the competitive exclusion principle, species less suited to compete for resources must either adapt or die out, although competitive exclusion is rarely found in natural ecosystems. Ecologists use a modified version of coupled logistic growth models for competing species, known as the Lotka-Volterra Competition model, to model interspecific competition.

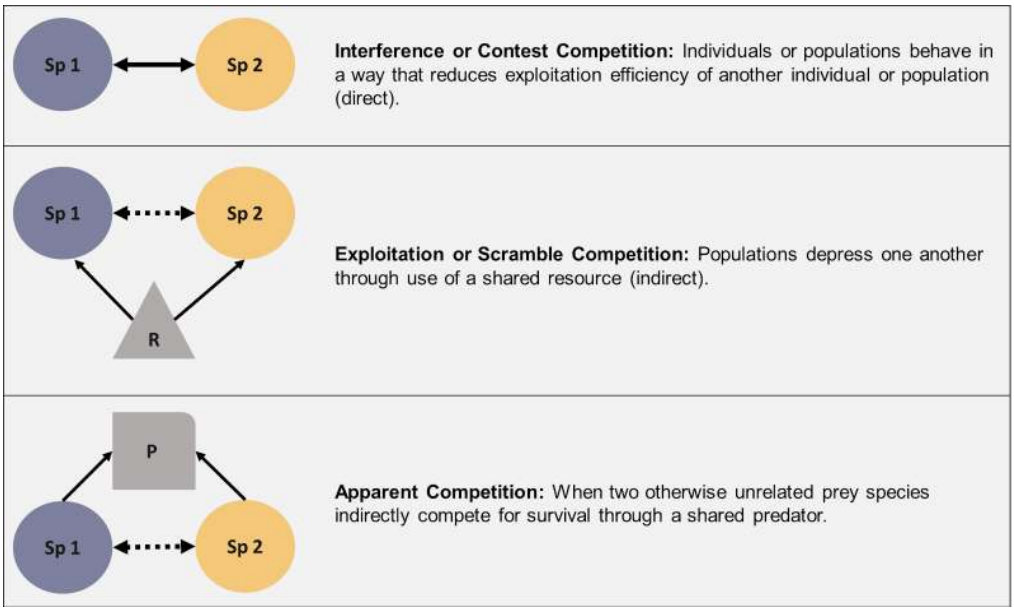


Figure 15.1.1: *The three different mechanisms of competition. Solid arrows indicate direct relationships, dashed lines represent indirect relationships. Developed by N. Gownaris.*

Video



Types of Competition

Interference Competition

During interference competition, also called contest competition, organisms of the same species or of two or more different species interact directly by fighting for scarce resources. For example, large aphids defend feeding sites on cottonwood leaves by ejecting smaller aphids from better sites. Male-male competition in red deer during rut is an example of interference competition that occurs within a species (intraspecific competition).



Figure 15.1.1: Male-male competition in red deer during rut is an example of interference competition within a species

Interference competition occurs directly between individuals via aggression when the individuals interfere with foraging, survival, reproduction of others, or by directly preventing their physical establishment in a portion of the habitat. An example of this can be seen between the ant *Novomessor cockerelli* and red harvester ants, where the former interferes with the ability of the latter to forage by plugging the entrances to their colonies with small rocks. Male bowerbirds, who create elaborate structures called *bowers* to attract potential mates, may reduce the fitness of their neighbors directly by stealing decorations from their structures.

In animals, interference competition is a strategy mainly adopted by larger and stronger organisms within a habitat. As such, populations with high interference competition have adult-driven generation cycles. At first, the growth of juveniles is stunted by larger adult competitors. However, once the juveniles reach adulthood, they experience a secondary growth cycle. Plants, on the other hand, primarily engage in interference competition with their neighbors through allelopathy, or the production of biochemicals.

Interference competition can be seen as a strategy that has a clear cost (injury or death) and benefit (obtaining resources that would have gone to other organisms). In order to cope with strong interference competition, other organisms often either do the same or engage in exploitation competition. For example, depending on the season, larger ungulate red deer males are competitively dominant due to interference competition. However, does and fawns have dealt with this through temporal resource partitioning — foraging for food only when adult males are not present.

Exploitation Competition

Exploitation competition, or scramble competition, occurs indirectly when organisms both use a common limiting resource or shared food item. Instead of fighting or exhibiting aggressive behavior in order to win resources, exploitative competition occurs when resource use by one organism depletes the total amount available for the other organism. These organisms might never interact directly, but compete by responding to changes in resource levels. Very obvious examples of this phenomenon include a diurnal species and a nocturnal species that nevertheless share the same resources, or a plant that competes with neighboring plants for light, nutrients, and space for root growth (Jensen 1987).

This form of competition typically rewards those organisms who claim the resource first. As such, exploitation competition is often size-dependent and smaller organisms are favored since smaller organisms typically have higher foraging rates. Since smaller organisms have an advantage when exploitative competition is important in an ecosystem, this mechanism of competition might lead to a juvenile-driven generation cycle: individual juveniles succeed and grow fast, but once they mature they are outcompeted by smaller organisms.

In plants, exploitative competition can occur both above- and below-ground. Aboveground, plants reduce the fitness of their neighbors by vying for sunlight. Plants consume nitrogen by absorbing it into their roots, making nitrogen unavailable to nearby plants. Plants that produce many roots typically reduce soil nitrogen to very low levels, eventually killing neighboring plants.

Exploitative competition has also been shown to occur both within species (intraspecific) and between different species (interspecific). Furthermore, many competitive interactions between organisms are some combination of exploitative and interference competition, meaning the two mechanisms are far from mutually exclusive. For example, a recent 2019 study found that the native thrips species *Frankliniella intonsa* was competitively dominant over an invasive thrips species *Frankliniella occidentalis* because it not only exhibited greater time feeding (exploitative competition) but also greater time guarding its resources (interference competition). Plants may also exhibit both forms of competition, not only scrambling for space for root growth but also directly inhibiting other plants' development through allelopathy.

Apparent Competition

Apparent competition occurs when two otherwise unrelated prey species indirectly compete for survival through a shared predator. This form of competition typically manifests in new equilibrium abundances of each prey species. For example, suppose there are two species (species A and species B), which are preyed upon by food-limited predator species C. Scientists observe an increase in the abundance of species A and a decline in the abundance of species B. In an apparent competition model, this relationship is found to be mediated through predator C; a population explosion of species A increases the abundance of predator species C due to a greater total food source. Since there are now more predators, species A and B would be hunted at higher rates than before. Thus, the success of species A was to the detriment of species B — not because they competed for resources, but because their increased numbers had indirect effects on the predator population.

Video



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15.2: Intraspecific (Single Species) Competition



Figure 15.2.1: *Male hartebeest locking horns and fiercely defending their territories, an example of direct competition.*

Intraspecific competition is an interaction in population ecology, whereby members of the same species compete for limited resources. This leads to a reduction in fitness for both individuals, but the more fit individual survives and is able to reproduce. By contrast, interspecific competition occurs when members of different species compete for a shared resource. Members of the same species have rather similar requirements for resources, whereas different species have a smaller contested resource overlap, resulting in intraspecific competition generally being a stronger force than interspecific competition.

Intraspecific competition does not just involve direct interactions between members of the same species (such as male deer locking horns when competing for mates) but can also include indirect interactions where an individual depletes a shared resource (such as a grizzly bear catching a salmon that can then no longer be eaten by bears at different points along a river).

When resources are infinite, intraspecific competition does not occur and populations can grow exponentially. Exponential population growth is exceedingly rare but has been documented, most notably in humans since 1900. Elephant (*Loxodonta africana africana*) populations in Kruger National Park (South Africa) also grew exponentially in the mid-1900s after strict poaching controls were put in place. However, prolonged exponential growth is rare in nature because resources are finite and so not every individual in a population can survive, leading to intraspecific competition for scarce resources. Individuals can compete for food, water, space, light, mates, or any other resource which is required for survival or reproduction. The resource must be limited for competition to occur; if every member of the species can obtain a sufficient amount of every resource then individuals do not compete and the population grows exponentially.

When resources are limited, an increase in population size reduces the quantity of resources available for each individual, reducing the per capita fitness of the population. As a result, the growth rate of a population slows as intraspecific competition becomes more intense, making it a negatively density-dependent process.

The falling population growth rate as population increases can be modeled effectively with the logistic growth model. The rate of change of population density eventually falls to zero, the point ecologists have termed the carrying capacity (K). However, a population can only grow to a very limited number within an environment. The carrying capacity, defined by the variable K, of an environment is the maximum number of individuals or species an environment can sustain and support over a longer period of time.

The logistic growth equation is an effective tool for modeling intraspecific competition despite its simplicity and has been used to model many real biological systems. Here x is the size of the population at a given time, r is the inherent per-capita growth rate, and K is the carrying capacity. At low population densities, $x(t)$ is much smaller than K and so the main determinant for population growth is just the per capita growth rate. However, as $N(t)$ approaches the carrying capacity the second term in the logistic equation becomes smaller, reducing the rate of change in population density. Eventually, the population size equals the carrying capacity, and the population growth rate equals zero.

$$\frac{dN}{dt} = rN\left(\frac{K-N}{K}\right)$$

dN/dt = rate of change of population density

N = population size at time *t*

r = per capita growth rate

K = carrying capacity

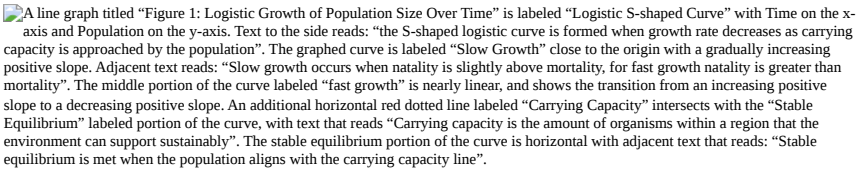


Figure 15.2.2: *This figure shows the growth of a population following a logistic curve, resulting in the S-shaped graph. This model reaches a stable equilibrium, sustaining the population at the carrying capacity as time continues. Developed by Nchisick under CC-BY-SA.*

The logistic growth curve (Figure 15.2.2) is initially very similar to the exponential growth curve. When population density is low, individuals are free from competition and can grow rapidly. However, as the population reaches its maximum (the carrying capacity), intraspecific competition becomes fiercer and the per capita growth rate slows until the population reaches a stable size. At the carrying capacity, the rate of change of population density is zero because the population is as large as possible based on the resources available. Experiments on *Daphnia* growth rates showed a striking adherence to the logistic growth curve. The inflection point in the *Daphnia* population density graph occurred at half the carrying capacity, as predicted by the logistic growth model.

In summary, the resources within an environment are limited. Therefore, the environment can only support a certain number of individuals before its resources completely diminish. Numbers larger than this will suffer a negative population growth until eventually reaching the carrying capacity, whereas populations smaller than the carrying capacity will grow until they reach it.

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15.3: Interspecific (Two Species) Competition



Figure 15.3.1: *Subadult male lion and spotted hyena in the Masai Mara. The two species share the same ecological niche and are thus in competition with each other.*

Interspecific competition may occur when individuals of two separate species share a limiting resource in the same area. If the resource cannot support both populations, then lowered fecundity, growth, or survival may result in at least one species. Interspecific competition has the potential to alter populations, communities, and the evolution of interacting species. An example among animals could be the case of cheetahs and lions; since both species feed on similar prey, they are negatively impacted by the presence of the other because they will have less food, however, they still persist together, despite the prediction that under competition one will displace the other. In fact, lions sometimes steal prey items killed by cheetahs. Potential competitors can also kill each other, in so-called 'intraguild predation'. For example, in southern California coyotes often kill and eat gray foxes and bobcats, all three carnivores sharing the same stable prey (small mammals).

Interspecific Competition: The Lotka-Volterra Model

Given two populations, *N*1 and *N*2, with logistic dynamics, the Lotka–Volterra formulation adds an additional term to account for the species' interactions. Thus the competitive Lotka–Volterra equations are:

Population 1:

$$\frac{dN_1}{d_t} = r_1 N_1 \left(\frac{K_1 - N_1 - a_{12} N_2}{K_1} \right)$$

Population 2:

$$\frac{dN_2}{d_t} = r_2 N_2 \left(\frac{K_2 - N_2 - a_{21} N_1}{K_2} \right)$$

Here, $\alpha 12$ represents the effect species 2 has on the population of species 1 and $\alpha 21$ represents the effect species 1 has on the population of species 2. These values do not have to be equal. Because this is the competitive version of the model, all interactions must be harmful (competition) and therefore all α-values are positive. Note that each species can have its own growth rate and carrying capacity. The Lotka-Volterra model for competition and how it is used to predict competitive outcomes is described in more detail in the Quantifying Competition section of this chapter.

Resource-Ratio Hypothesis (R* rule)

The **R* rule** (also called the **resource-ratio hypothesis**) is a hypothesis that attempts to predict which species will become dominant as the result of competition for resources. It predicts that if multiple species are competing for a single limiting resource, then whichever species can survive at the lowest **equilibrium resource level** (i.e., the **R***) can outcompete all other species . If two species are competing for two resources, then coexistence is only possible if each species has a lower R* on one of the resources.

For example, two phytoplankton species may be able to coexist if one is more limited by nitrogen, and the other is more limited by phosphorus.

Consider a community with multiple species. We will assume that each species competes for a single resource, and ignore the effects of interference or apparent competition. Each population increases by consuming resources, and declines when resources are too scarce. For example, we could model their population dynamics as

$$\frac{dN_j}{dt} = N_j \left(a_j R - d\right)$$

$$\frac{dR}{dt} = r - R\sum_j a_j N_j$$

where N_j is the density of species j, R is the density of the resource, a is the rate at which species j eats the resource, d is species j's death rate, and r is the rate at which resources grow when not consumed. It is easy to show that when species j is at equilibrium by itself (i.e., $dN_j/dt = 0$), that the equilibrium resource density, R^*_j, is

$$R_j^* = d/a_j$$

When $R > R^*_j$, species j's population will increase; when R is less than R^*_j, species j's population will decline. Because of this, the species with the lowest R^* will eventually dominate. Consider the two species case, where $R^*_1 < R^*_2$. When species 2 is at equilibrium, $R = R^*_2$, and species 1's population will be increasing. When species 1 is at equilibrium, $R = R^*_1$, and species 2's population will be decreasing.

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15.4: Ecological Consequences of Competition

Competitive Exclusion

The **competitive exclusion principle** postulates that two species that compete for the same limited resource cannot coexist at constant population values. When one species has even the slightest advantage over another, the one with the advantage will dominate in the long term (Figure 15.4.1). This leads either to the extinction of the weaker competitor or to an evolutionary or behavioral shift toward a different ecological niche. The principle has been paraphrased in the maxim "complete competitors cannot coexist".

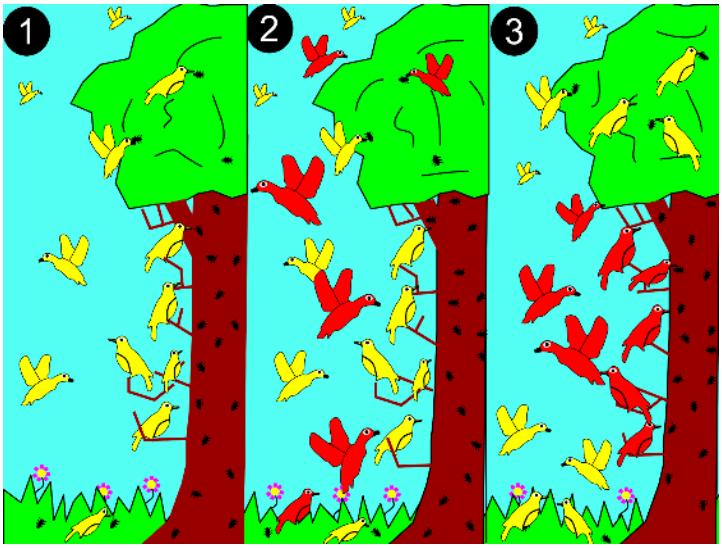


Figure 15.4.1: *1: A smaller (yellow) species of bird forages across the whole tree. 2: A larger (red) species competes with the yellow species for resources. 3: Red dominates in the middle for the more abundant resources. Yellow shifts to a new niche, avoiding competition.*

Georgy Gause formulated the law of competitive exclusion based on laboratory competition experiments using two species of *Paramecium*, *P. aurelia* and *P. caudatum* (Figure 15.4.2). The conditions were to add fresh water every day and input a constant flow of food. Although *P. caudatum* initially dominated, *P. aurelia* recovered and subsequently drove *P. caudatum* extinct via exploitative resource competition. However, Gause was able to let the *P. caudatum* survive by differing the environmental parameters (food, water). Thus, Gause's law is valid only if the ecological factors are constant.

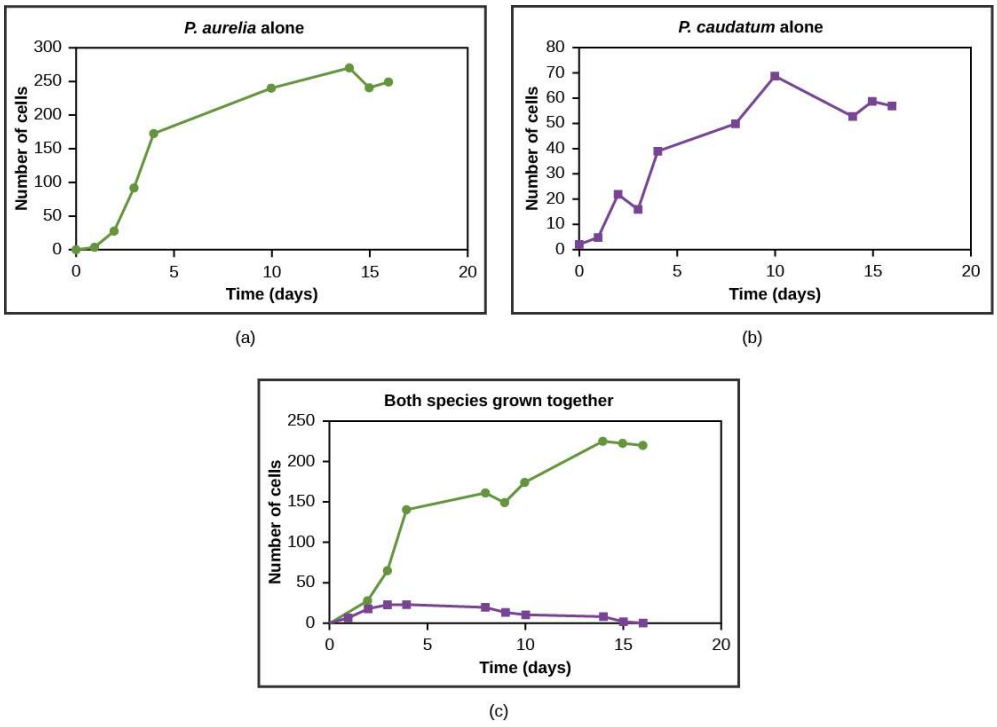
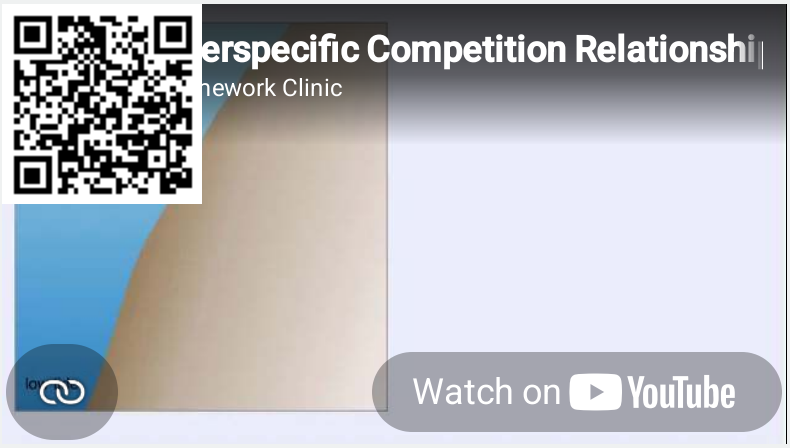


Figure 15.4.2: *Paramecium aurelia and Paramecium caudatum grow well individually, but when they compete for the same resources, P. aurelia outcompetes P. caudatum.*

Competitive exclusion is predicted by mathematical and theoretical models such as the Lotka–Volterra models of competition. However, competitive exclusion is rarely observed in natural ecosystems and many biological communities appear to violate Gause's law. The best-known example is the so-called "paradox of the plankton". All plankton species live on a very limited number of resources, primarily solar energy and minerals dissolved in the water. According to the competitive exclusion principle, only a small number of plankton species should be able to coexist on these resources. Nevertheless, large numbers of plankton species coexist within small regions of open sea.

Video



Niche Differentiation

Niche differentiation (also known as **niche separation** and **niche partitioning**) refers to the process by which competing species use the environment differently in a way that helps them to coexist. When two species differentiate their niches, they tend to

compete less strongly, and are thus more likely to coexist. Species can differentiate their niches in many ways, such as by consuming different foods, or using different areas of the environment.

As an example of niche partitioning, several anole lizards in the Caribbean islands share common diets—mainly insects. They avoid competition by occupying different physical locations. Although these lizards might occupy different locations, some species can be found inhabiting the same range, with up to 15 in certain areas. For example, some live on the ground while others are arboreal. Species who live in different areas compete less for food and other resources, which minimizes competition between species. However, species who live in similar areas typically compete with each other (Figure 15.4.3).



Figure 15.4.3: *Niche differentiation by size: greater duckweed, lesser duckweed and rootless dwarf duckweed*

Competing species can partition their niche in different ways. This list is not exhaustive but illustrates several classic examples.

- **Resource Partitioning** is the phenomenon where two or more species divide out resources like food, space, resting sites etc. to coexist. For example, some lizard species appear to coexist because they consume insects of differing sizes. Alternatively, species can coexist on the same resources if each species is limited by different resources, or differently able to capture resources. Different types of phytoplankton can coexist when different species are differently limited by nitrogen, phosphorus, silicon, and light. In the Galapagos Islands, finches with small beaks are more able to consume small seeds, and finches with large beaks are more able to consume large seeds. If a species' density declines, then the food it most depends on will become more abundant (since there are so few individuals to consume it). As a result, the remaining individuals will experience less competition for food. Although "resource" generally refers to food, species can partition other non-consumable objects, such as parts of the habitat. For example, warblers are thought to coexist because they nest in different parts of trees. Species can also partition a habitat in a way that gives them access to different types of resources. As previously stated, anole lizards appear to coexist because each uses different parts of the forests as perch locations. This likely gives them access to different species of insects.
- **Predator Partitioning** occurs when species are attacked differently by different predators (or natural enemies more generally). For example, trees could differentiate their niche if they are consumed by different species of specialist herbivores, such as herbivorous insects. If a species' density declines, so too will the density of its natural enemies, giving it an advantage. Thus, if each species is constrained by different natural enemies, they will be able to coexist. Early work focused on specialist predators; however, more recent studies have shown that predators do not need to be pure specialists, they simply need to affect each prey species differently.
- **Conditional Differentiation** (sometimes called **temporal niche partitioning**) occurs when species differ in their competitive abilities based on varying environmental conditions. For example, in the Sonoran Desert, some annual plants are more successful during wet years, while others are more successful during dry years. As a result, each species will have an advantage in some years, but not others. When environmental conditions are most favorable, individuals will tend to compete most strongly with members of the same species. For example, in a dry year, dry-adapted plants will tend to be most limited by other dry-adapted plants.
- **Competition-Predation Trade-Off** Species can differentiate their niche via a competition-predation trade-off if one species is a better competitor when predators are absent, and the other is better when predators are present. Defenses against predators, such as toxic compounds or hard shells, are often metabolically costly. As a result, species that produce such defenses are often poor competitors when predators are absent. Species can coexist through a competition-predation trade-off if predators are more abundant when the less defended species is common, and less abundant if the well-defended species is common. This effect has

been criticized as being weak because theoretical models suggest that only two species within a community can coexist because of this mechanism.

Coexistence

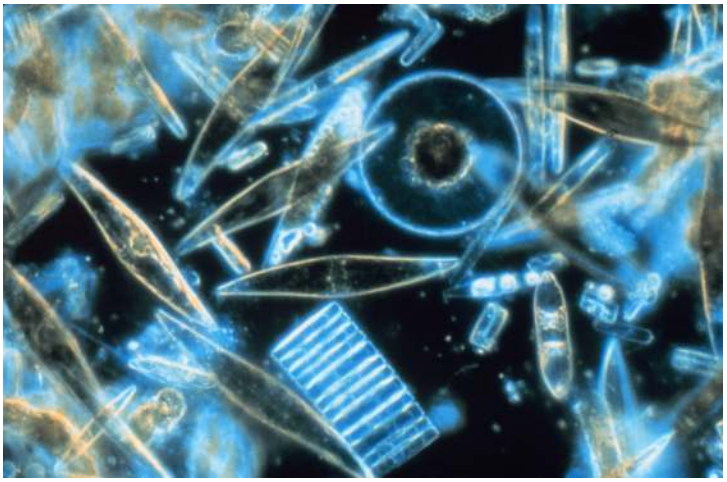


Figure 15.4.4: *Coexistence theory attempts to explain the paradox of the plankton - how can ecologically similar species coexist without competitively excluding each other?*

Coexistence theory is a framework to understand how competitor traits can maintain species diversity and stave-off competitive exclusion even among similar species living in ecologically similar environments (Figure 15.4.4).

Coexistence theory explains the stable coexistence of species as an interaction between two opposing forces: fitness differences between species, which should drive the best-adapted species to exclude others within a particular ecological niche, and stabilizing mechanisms, which maintains diversity via niche differentiation. For many species to be stabilized in a community, population growth must be negative density-dependent, i.e. all participating species have a tendency to increase in density as their populations decline. In such communities, any species that becomes rare will experience positive growth, pushing its population to recover and making local extinction unlikely. As the population of one species declines, individuals of that species tend to compete predominantly with individuals of other species. Thus, the tendency of a population to recover as it declines in density reflects reduced intraspecific competition (within-species) relative to interspecific competition (between-species) the signature of niche differentiation.



Figure 15.4.5: *Groundhog and a raccoon eating together*

Two qualitatively different processes can help species to coexist: a reduction in average fitness differences between species or an increase in niche differentiation between species. These two factors have been termed equalizing and stabilizing mechanisms, respectively. For species to coexist, any fitness differences that are not reduced by equalizing mechanisms must be overcome by stabilizing mechanisms.

- **Equalizing mechanisms** reduce fitness differences between species. As its name implies, these processes act in a way that merge the competitive abilities of multiple species closer together. Equalizing mechanisms affect interspecific competition (the competition between individuals of different species). For example, when multiple species compete for the same resource, competitive ability is determined by the minimum level of resources a species needs to maintain itself (known as an R*, or equilibrium resource density). Thus, the species with the lowest R* is the best competitor and excludes all other species in the absence of any niche differentiation. Any factor that reduces the differences in R* level between species (like increased harvest of the dominant competitor) is classified as an equalizing mechanism. Environmental variation (which is the focus of the Intermediate Disturbance Hypothesis) can be considered an equalizing mechanism. Since the fitness of a given species is intrinsically tied to a specific environment, when that environment is disturbed (e.g. through storms, fires, volcanic eruptions, etc.) some species may lose components of their competitive advantage which were useful in the previous version of the environment.
- **Stabilizing mechanisms** promote coexistence by concentrating intraspecific competition relative to interspecific competition. In other words, these mechanisms "encourage" an individual to compete more with other individuals of its own species, rather than with individuals of other species (Figure 15.4.5). Stabilizing mechanisms increase the low-density growth rate of all species. Resource partitioning (a type of niche differentiation) is a stabilizing mechanism because interspecific competition is reduced when different species primarily compete for different resources. Similarly, if species are differently affected by environmental variation (e.g., soil type, rainfall timing, etc.), this can create a stabilizing mechanism called the storage effect. The theory proposes one way for multiple species to coexist: in a changing environment, no species can be the best under all conditions. Instead, each species must have a unique response to varying environmental conditions, and a way of buffering against the effects of bad years. The storage effect gets its name because each population "stores" the gains in good years or microhabitats (patches) to help it survive population losses in bad years or patches.

Character Displacement

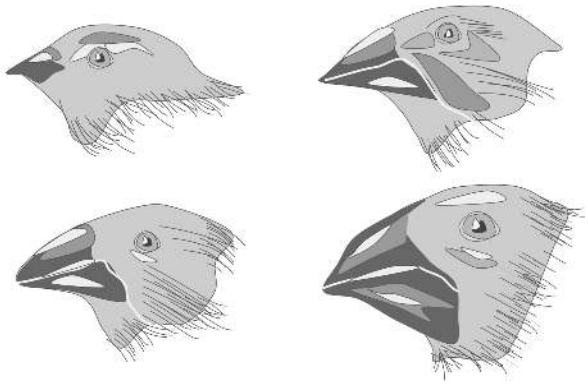


Figure 15.4.6: Character displacement among finches of the Galapagos.

Character displacement occurs when similar species that live in the same geographical region and occupy similar niches differentiate in order to minimize niche overlap and avoid competitive exclusion. Several species of Galapagos finches display character displacement (Figure 15.4.6). Each closely related species differs in beak size and beak depth, allowing them to coexist in the same region since each species eats a different type of seed: the seed best fit for its unique beak. The finches with the deeper, stronger beaks consume large, tough seeds, while the finches with smaller beaks consume the smaller, softer seeds.

Character displacement is the phenomenon where differences among similar species whose distributions overlap geographically are accentuated in regions where the species co-occur, but are minimized or lost where the species' distributions do not overlap. This pattern results from evolutionary change driven by biological competition among species for a limited resource (e.g. food). The rationale for character displacement stems from the competitive exclusion principle, which contends that to coexist in a stable environment two competing species must differ in their respective ecological niche; without differentiation, one species will eliminate or exclude the other through competition.

For example, Darwin's finches can be found alone or together on the Galapagos Islands. Both species' populations actually have more individuals with intermediate-sized beaks when they live on islands without the other species present. However, when both

species are present on the same island, competition is intense between individuals that have intermediate-sized beaks of both species because they all require intermediate sized seeds. Consequently, individuals with small and large beaks have greater survival and reproduction on these islands than individuals with intermediate-sized beaks. Different finch species can coexist if they have traits—for instance, beak size—that allow them to specialize on particular resources. When *Geospiza fortis* and *Geospiza fuliginosa* are present on the same island, *G. fuliginosa* tends to evolve a small beak and *G. fortis* a large beak. The observation that competing species' traits are more different when they live in the same area than when competing species live in different areas is called character displacement. For the two finch species, beak size was displaced: beaks became smaller in one species and larger in the other species.

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15.5: Quantifying Competition Using the Lotka-Volterra Model

Real populations do not exist in isolation, but share habitats with populations of other species. In many cases, coexisting species will interact by interspecific competition, predation, parasitism, mutualism, or other ecological interactions. More realistic models must take such interactions into account. In the 1920s, Vito Volterra and Alfred Lotka (1932) independently developed models of **interspecific competition** (competition between two species), and investigated the conditions that would permit competing species to coexist indefinitely.

An important ecological generalization, the **competitive exclusion principle**, has grown out of the Lotka-Volterra model and from other sources. This principle states that *two species cannot coexist unless their niches are sufficiently different that each limits its own population growth more than it limits that of the other*. In other words, if there is too much niche overlap, one species will competitively exclude the other. In reality, whether two species coexist depends not only on their competitive interactions with each other, but also on their interactions with the abiotic environment and with other species not included in this simple model. Nevertheless, the competitive exclusion principle has proven fruitful in stimulating research and understanding ecological interactions in the natural world.

In broad terms, the questions Lotka and Volterra asked were:

- What will happen to the population dynamics of these two populations, given various values of the model parameters?
- Are there parameter values that will produce a winner and a loser—one population that persists while the other goes extinct? This would be competitive exclusion.
- Will other values result in coexistence, in which both competing populations persist indefinitely?

Model Development – Starting with One Species

The logistic model of population growth focuses on **intraspecific competition** (competition between individuals of the same species). To keep things (relatively) simple, we will develop our model of interspecific competition beginning with this form of the logistic model:

$$\frac{dN_1}{d_t} = r_1 N_1 \left(\frac{K_1 - N_1}{K_1} \right)$$

where K is the carrying capacity, or largest sustainable population. The value of K is set by available resources and by each individual's resource demand. This version of the logistic model has intraspecific competition built into it in the term $(K - N_t)/K$. This term reduces the population growth rate in response to the addition of each new member of the population, representing the reduction in per capita birth rate, and increase in per capita death rate, caused by competition for limited resources.

The Lotka-Volterra model of interspecific competition builds on the logistic model of a single population. It begins with a separate logistic model of the population of each of the two, competing species.

Population 1:

$$\frac{dN_1}{d_t} = r_1 N_1 \left(\frac{K_1 - N_1}{K_1} \right)$$

Population 2:

$$\frac{dN_2}{d_t} = r_2 N_2 \left(\frac{K_2 - N_2}{K_2} \right)$$

Note the use of subscripts 1 and 2 to denote which species' population is being modeled. Each population has its own rate of increase *r* and carrying capacity *K*, and these may differ between the two species.

Model Development – Coupling Two Competitors

Next, we build interspecific competition into each of these equations. We assume that each new member of Population 1 reduces resources available to each member of Population 2, and thus reduces population growth rate. Additionally, new members of Population 2 will also reduce resources available to members of Population 1—this is, after all, the meaning of interspecific competition.

The simplest way to model this would be to modify the $(K_1 - N_{1,t})/K$ term into $(K_1 - N_{1,t} - N_{2,t})/K_1$. However, this assumes that each additional member of Population 2 will affect Population 1 exactly as much as an additional member of Population 1. That is not necessarily the case, so we multiply $N_{2,t}$ in this term by a **competition coefficient**, α_{12} to express how much effect each additional member of Population 2 has on Population 1, relative to the effect of a new member of Population 1. We modify the model for Population 2 in a parallel way. The resulting Lotka-Volterra model of two-species competition is:

Population 1:

$$\frac{dN_1}{d_t} = r_1 N_1 \left(\frac{K_1 - N_1 - a_{12} N_2}{K_1} \right)$$

Population 2:

$$\frac{dN_2}{d_t} = r_2 N_2 \left(\frac{K_2 - N_2 - a_{21} N_1}{K_2} \right)$$

Note the subscripts on the competition coefficients: α_{12} expresses the effect of one member of Population 2 on the growth rate of Population 1; α_{21} expresses the effect of one member of Population 1 on the growth rate of Population 2.

The value of the competition coefficient tells us something about the relative importance of interspecific and intraspecific competition on the population dynamics of a species.

- When the competition coefficient is less than 1, intraspecific competition has a stronger per capita impact on resource availability for that species.
- When the competition coefficient is greater than 1, interspecific competition has a stronger per capita impact on resource availability for that species.
- When the competition coefficient is equal to 1, inter and intraspecific competition have a similar per capita impact on resource availability for that species.

Equilibrium Solutions for Coupled Competitors

To understand the outcome of competition between these two species, we must first find the equilibrium solutions to the coupled equations above. The equilibrium is the population size at which the population stops growing. We can solve for this equilibrium by setting dN/dt for each species to zero and solving for N.

For Population 1, for example:

$$\mathrm{N}_1 = K_1 - a_{12}N_2$$

The resulting equation is the equation of a line, y = a + bx. We call this line a **zero net growth isocline**, or **ZNGI**, because anywhere along it, Population 1 has zero net growth. In other words, this is an equilibrium solution for Population 1.

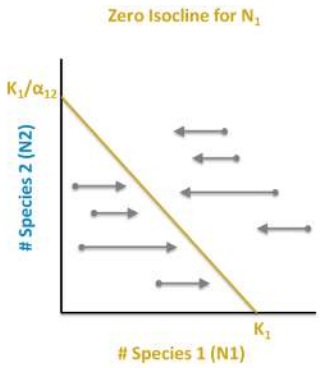
Just as *x* and *y* in the general linear equation *y* = *a* + *bx* can be used as coordinates for graphing, so we can use *N*1 and *N*2 as coordinates to graph each species ZNGI. We can graph this isocline by finding any two points along it and connecting them with a straight line.

Two convenient points are where $N_{2,t} = 0$ and where $N_{1,t} = 0$. **If we solve for these intercepts, we wind up with the following two coordinates for Population 1: [0, K_1/a_{12}] (setting x, or the size of Population 1, to 0) and [K_1, 0] (setting y, or the population size of Population 2, to 0).** In words, if there are no members of Population 2 in the habitat, Population 1 will stabilize at its own carrying capacity, *K*1. This seems a reasonable solution. If there are no members of Population 1, Population 2 will stabilize at the carrying capacity of Population 1 accounting for the relative per capita resource requirements of Population 2 relative to Population 1. These points can be plotted and connected to visualize the ZNGI.

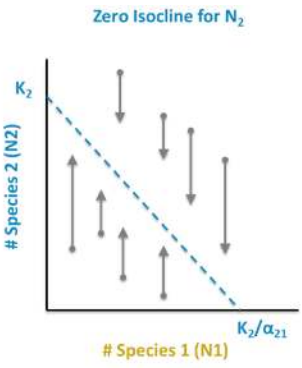
The same is done for Population 2:

$$\mathrm{N}_2 = K_2 - a_{21}N_1$$

This results in the following ZNGI coordinates: [0, K_2] and [K_2/a_{21},0].



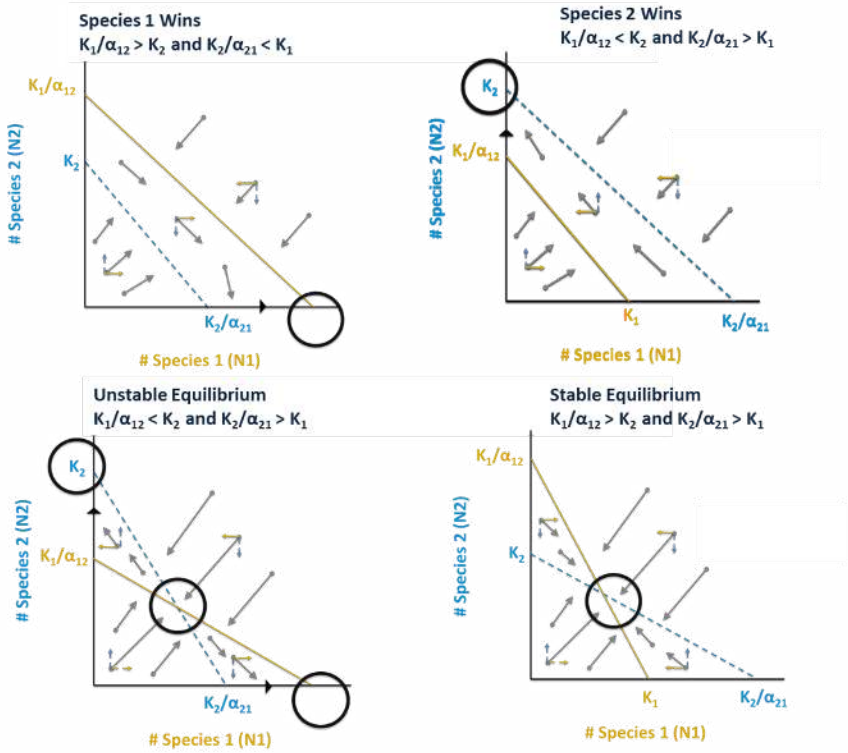
$$N_1 = K_1 - a_{12}N_2$$



$$N_2 = K_2 - a_{21}N_1$$

To determine the outcome of competition, we must be able to find the ZNGI lines and the initial sizes of each population and graph them. We can graph the populations of the two species at any time by a point on a graph. Population 1 should always be plotted on the x-axis and Population 2 is on the y-axis. If the point falls below (Population 1) and/or to the left (Population 2) of a species' isocline, that population will continue to increase. If the point falls above (Population 1) and/or to the right (Population 2) of a species' isocline, that population will decrease. This will continue to occur as the coupled populations change sizes, and the point describing the two populations will trace some trajectory across the graph, eventually reaching an equilibrium of coexistence or competition exclusion.

Notice that time does not appear on either axis of this graph. The plots above are called **phase diagrams**, and the space bounded by its axes is called **phase space**. You can plot the trajectory of two changing populations through the phase space and from that determine whether one species excludes the other, or if they coexist.



A Quick Summary of Coupled Interspecific Competition Models

Based on the Logistic Model:

- Alone, Species 1 and 2 increase to their K
- Species 1 and 2 reduce each others' K

Outcomes Depend On:

- Competition coefficient
- Species 1 and Species 2 carrying capacity
- Species 1 and Species 2 starting population size

Steps to Determining Outcomes:

- Find and plot Species 1 isocline (K_1 on x; K_1/α_{12} on y)
- Find and plot Species 2 isocline (K_2/α_{21} on x; K_2 on y)
- Plot initial population size
- Determine vectors and outcome

Models Review - Exponential, Logistic, Competition

Exponential (Review) – No Carrying Capacity

$$\frac{dN_1}{d_t} = r_1 N_1$$

r_1 = intrinsic growth rate of species 1

N_1 = population size of species 1

Logistic (Review) – Single Species, Carry Capacity

$$\frac{dN_1}{d_t} = r_1 N_1 \left(\frac{K_1 - N_1}{K_1} \right)$$

K_1 = carrying capacity of species 1 (when K = N, dN/dt = 0)

Competition – Two Species Logistic Model, Equations Linked

Population 1:

$$\frac{dN_1}{d_t} = r_1 N_1 \left(\frac{K_1 - N_1 - a_{12} N_2}{K_1} \right)$$

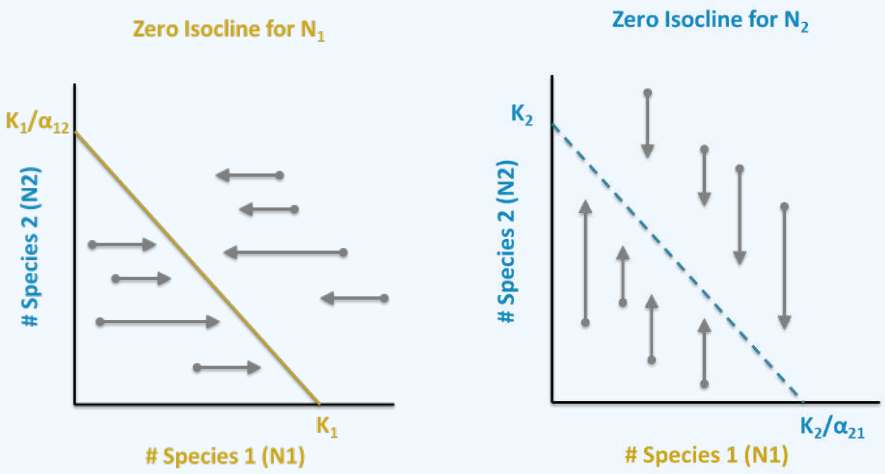
Population 2:

$$\frac{dN_2}{d_t} = r_2 N_2 \left(\frac{K_2 - N_2 - a_{21} N_1}{K_2} \right)$$

α_{12} or α = a measure of the per capita effect of species 2 on the growth of species 1

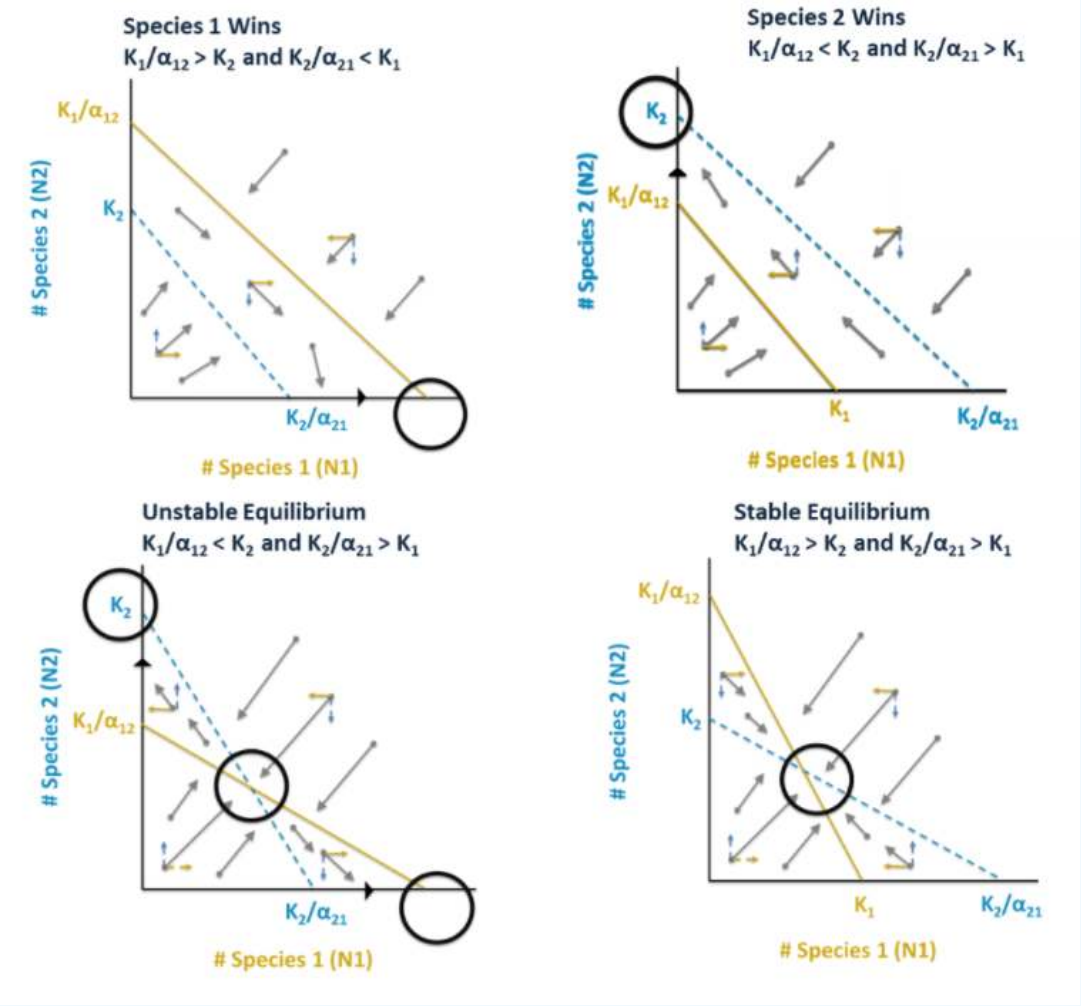
α_{21} or β = a measure of the per capita effect of species 1 on the growth of species 2

Species 1 and Species 2 Isoclines



$$N_1 = K_1 - a_{12}N_2 \quad N_2 = K_2 - a_{21}N_1$$

Species 1 and Species 2 Outcomes



Summary

Summary to be added

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15.6: References and Attributions

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CHAPTER OVERVIEW

Chapter 16: Antagonistic Interactions

Video



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Summary

Summary to be added

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16.1: Predation

Introduction

Predation is a biological interaction where one organism, the **predator**, kills and eats another organism, its **prey** (Figure 16.1.1).

Video

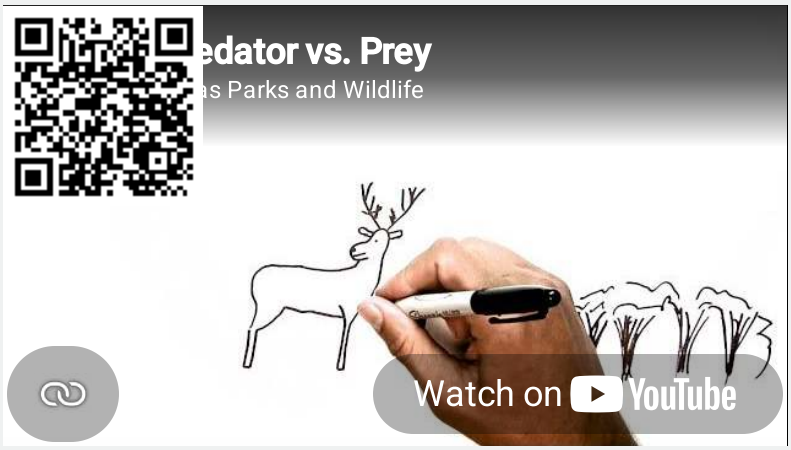




Figure 16.1.1: (Left) *A solitary predator: a polar bear feeds on a bearded seal it has killed. (Right) Social predators: meat ants cooperate to feed on a cicada far larger than themselves.*

It is one of a family of common feeding behaviors that includes parasitism and micropredation (which usually do not kill the host) and parasitoidism (which always does, eventually) (Figure 16.1.2). It is distinct from scavenging on dead prey, though many predators also scavenge. Predation and herbivory overlap because seed predators and destructive frugivores kill their "prey".

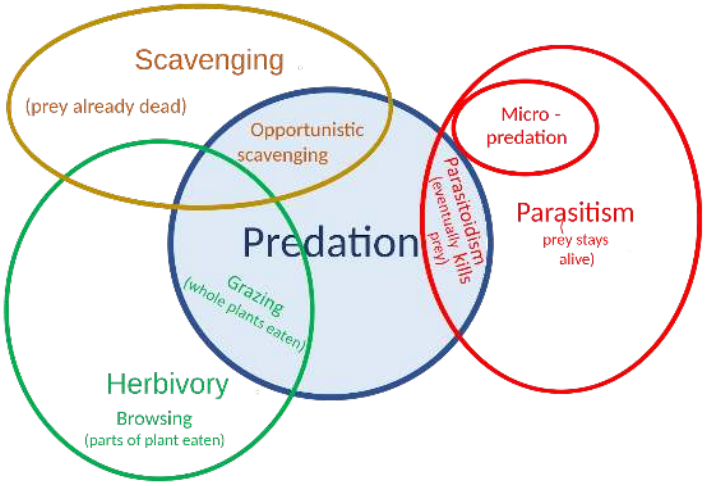


Figure 16.1.2: *Relation of predation to other feeding strategies*

The concept of predation is broad, defined differently in different contexts, and includes a wide variety of feeding methods; and some relationships that result in the prey's death are not generally called predation. A parasitoid, such as an ichneumon wasp, lays its eggs in or on its host; the eggs hatch into larvae, which eat the host, and it inevitably dies (Figure 16.1.3). Zoologists generally call this a form of parasitism, though conventionally parasites are thought not to kill their hosts. A predator can be defined to differ from a parasitoid in that it has many prey, captured over its lifetime, whereas a parasitoid's larva has just one, or at least has its food supply provisioned for it on just one occasion.



Figure 16.1.3: *Spider wasps paralyze and eventually kill their hosts, but are considered parasitoids, not predators.*

There are other difficult and borderline cases. Micropredators are small animals that, like predators, feed entirely on other organisms; they include fleas and mosquitoes that consume blood from living animals, and aphids that consume sap from living plants. However, since they typically do not kill their hosts, they are now often thought of as parasites. Animals that graze on phytoplankton or mats of microbes are predators, as they consume and kill their food organisms; but herbivores that browse leaves are not, as their food plants usually survive the assault. Scavengers, organisms that only eat organisms found already dead, are not predators, but many predators such as the jackal and the hyena scavenge when the opportunity arises. Among invertebrates, social wasps (yellowjackets) are both hunters and scavengers of other insects.

Predators are adapted and often highly specialized for hunting, with acute senses such as vision, hearing, or smell. Many predatory animals, both vertebrate and invertebrate, have sharp claws or jaws to grip, kill, and cut up their prey. Other adaptations include stealth and aggressive mimicry that improve hunting efficiency.

When prey is detected, the predator assesses whether to attack it. Predators may actively search for or pursue prey (**pursuit predation**) or sit and wait for prey (**ambush predation**), often concealed, prior to attack. If the attack is successful, the predator kills the prey, removes any inedible parts like the shell or spines, and eats it.

Predation has a powerful selective effect on prey, and the prey develop antipredator adaptations such as warning coloration, alarm calls and other signals, camouflage, mimicry of well-defended species, and defensive spines and chemicals. Sometimes predator and prey find themselves in an **evolutionary arms race**, a cycle of adaptations and counter-adaptations.

Foraging

To feed, a predator must search for, pursue and kill its prey. These actions form a foraging cycle (Figure 16.1.4). The predator must decide where to look for prey based on its geographical distribution; and once it has located prey, it must assess whether to pursue it or wait for a better choice. If it chooses pursuit, its physical capabilities determine the mode of pursuit (e.g., ambush or pursuit). Having captured the prey, it may also need to expend energy *handling* it (e.g., killing it, removing any shell or spines, and ingesting it).

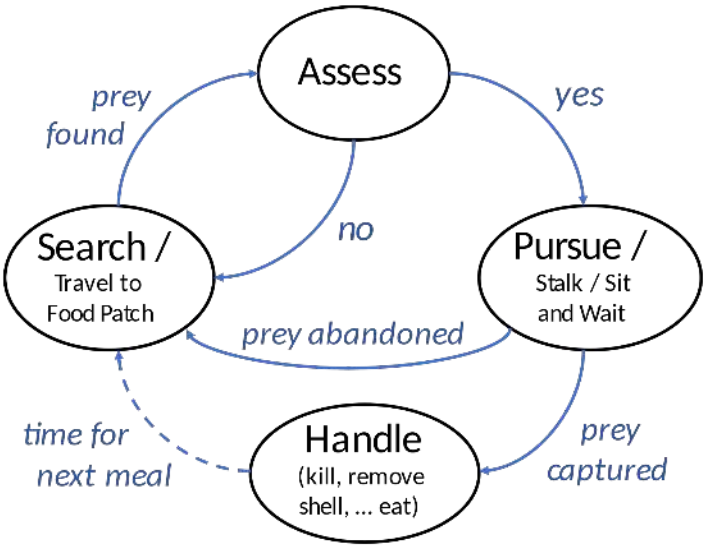


Figure 16.1.4: *A basic foraging cycle for a predator, with some variations indicated (Kramer 2001).*

Search

Predators have a choice of search modes ranging from *sit-and-wait* to *active* or *widely foraging*. The sit-and-wait method is most suitable if the prey are dense and mobile, and the predator has low energy requirements (Figure 16.1.5). Wide foraging expends more energy, and is used when prey is sedentary or sparsely distributed. There is a continuum of search modes with intervals between periods of movement ranging from seconds to months. Sharks, sunfish, insectivorous birds and shrews are almost always moving while web-building spiders, aquatic invertebrates, praying mantises and kestrels rarely move. In between, plovers and other shorebirds, freshwater fish including crappies, and the larvae of coccinellid beetles (ladybirds), alternate between actively searching and scanning the environment.



Figure 16.1.5: *Seven-spot ladybirds select plants of good quality for their aphid prey.*

Prey distributions are often clumped, and predators respond by looking for *patches* where prey is dense and then searching within patches (Kramer 2001). Where food is found in patches, such as rare shoals of fish in a nearly empty ocean, the search stage requires the predator to travel for a substantial time, and to expend a significant amount of energy, to locate each food patch. For example, the black-browed albatross regularly makes foraging flights to a range of around 700 kilometers (430 miles), up to a maximum foraging range of 3,000 kilometers (1,860 miles) for breeding birds gathering food for their young (Figure 16.1.6). With static prey, some predators can learn suitable patch locations and return to them at intervals to feed.



Figure 16.1.5: *The black-browed albatross regularly flies hundreds of kilometers across the nearly empty ocean to find patches of food.*

Assessment

Having found prey, a predator must decide whether to pursue it or keep searching. The decision depends on the costs and benefits involved. A bird foraging for insects spends a lot of time searching but capturing and eating them is quick and easy, so the efficient strategy for the bird is to eat every palatable insect it finds. By contrast, a predator such as a lion or falcon finds its prey easily but capturing it requires a lot of effort. In that case, the predator is more selective (Pianka 2011).

One of the factors to consider is size. Prey that is too small may not be worth the trouble for the amount of energy it provides. Too large, and it may be too difficult to capture. For example, a mantid captures prey with its forelegs and they are optimized for grabbing prey of a certain size. Mantids are reluctant to attack prey that is far from that size. There is a positive correlation between the size of a predator and its prey.

Capture

To capture prey, predators have a spectrum of pursuit modes that range from overt chase (pursuit predation) to a sudden strike on nearby prey (ambush predation).

Ambush

Ambush, or sit-and-wait predators, are carnivorous animals that capture prey by stealth or surprise. In animals, ambush predation is characterized by the predator's scanning the environment from a concealed position until prey is spotted, and then rapidly executing a fixed surprise attack. Vertebrate ambush predators include frogs, fish such as the angel shark, the northern pike, and the eastern frogfish. Among the many invertebrate ambush predators are trapdoor spiders and Australian Crab spiders on land and mantis shrimps in the sea. Ambush predators often construct a burrow in which to hide, improving concealment at the cost of reducing their field of vision. Some ambush predators also use lures to attract prey within striking range. The capturing movement has to be rapid to trap the prey, given that the attack is not modifiable once launched.



Figure 16.1.7: (Left) *A western green lizard ambushes its grasshopper prey. (Right) A trapdoor spider waiting in its burrow to ambush its prey*

Pursuit

In pursuit predation, predators chase fleeing prey. If the prey flees in a straight line, capture depends only on the predator's being faster than the prey. If the prey maneuvers by turning as it flees, the predator must react in real-time to calculate and follow a new intercept path as it closes on the prey. Many pursuit predators use camouflage to approach the prey as close as possible unobserved (stalking) before starting the pursuit. Pursuit predators include terrestrial mammals such as humans, African wild dogs, spotted hyenas and wolves; marine predators such as dolphins, orcas, and many predatory fishes, such as tuna; predatory birds (raptors) such as falcons; and insects such as dragonflies (Figure 16.1.8). Pursuit predators may be social, like the lion and wolf that hunt in groups, or solitary.

An extreme form of pursuit is endurance or persistence hunting, in which the predator tires out the prey by following it over a long distance, sometimes for hours at a time. The method is used by human hunter-gatherers and by canids such as African wild dogs and domestic hounds. The African wild dog is an extreme persistence predator, tiring out individual prey by following them for many miles at relatively low speed.

A specialized form of pursuit predation is the lunge feeding of baleen whales. These very large marine predators feed on plankton, especially krill, diving and actively swimming into concentrations of plankton, and then taking a huge gulp of water and filtering it through their feathery baleen plates.



Figure 16.1.8: (Left) *Humpback whales are lunge feeders, filtering thousands of krill from seawater and swallowing them alive.* (Right) *Dragonflies, like this common clubtail with captured prey, are invertebrate pursuit predators.*

Handling

Once the predator has captured the prey, it has to handle it: very carefully if the prey is dangerous to eat, such as if it possesses sharp or poisonous spines, as in many prey fish. Some catfish such as the *Ictaluridae* have spines on the back (dorsal) and belly (pectoral) which lock in the erect position; as the catfish thrashes about when captured, these could pierce the predator's mouth, possibly fatally (Figure 16.1.9). Some fish-eating birds like the osprey avoid the danger of spines by tearing up their prey before

eating it. Some prey may also be time-consuming to handle, such as clams or other bivalves that are difficult for predators to crush or open (Figure 16.1.9).



Figure 16.1.9: (Left) *Catfish has sharp dorsal and pectoral spines which it holds erect to discourage predators such as herons which swallow prey whole. (Right) Osprey tears its fish prey apart, avoiding dangers such as sharp spines.*

Predator Adaptations

Physical adaptations

Under the pressure of natural selection, predators have evolved a variety of physical adaptations for detecting, catching, killing, and digesting prey. These include speed, agility, stealth, sharp senses, claws, teeth, filters, and suitable digestive systems (Figure 16.1.10).

For detecting prey, predators have well-developed vision, smell, or hearing. Predators as diverse as owls and jumping spiders have forward-facing eyes, providing accurate binocular vision over a relatively narrow field of view, whereas prey animals often have less acute all-round vision. Animals such as foxes can smell their prey even when it is concealed under 2 feet (60 cm) of snow or earth. Many predators have acute hearing, and some such as echolocating bats hunt exclusively by active or passive use of sound.

Predators including big cats, birds of prey, and ants share powerful jaws, sharp teeth, or claws which they use to seize and kill their prey. Some predators such as snakes and fish-eating birds like herons and cormorants swallow their prey whole; some snakes can unhinge their jaws to allow them to swallow large prey, while fish-eating birds have long spear-like beaks that they use to stab and grip fast-moving and slippery prey. Fish and other predators have developed the ability to crush or open the armored shells of molluscs.

Many predators are powerfully built and can catch and kill animals larger than themselves; this applies as much to small predators such as ants and shrews as to big and visibly muscular carnivores like the cougar and lion.

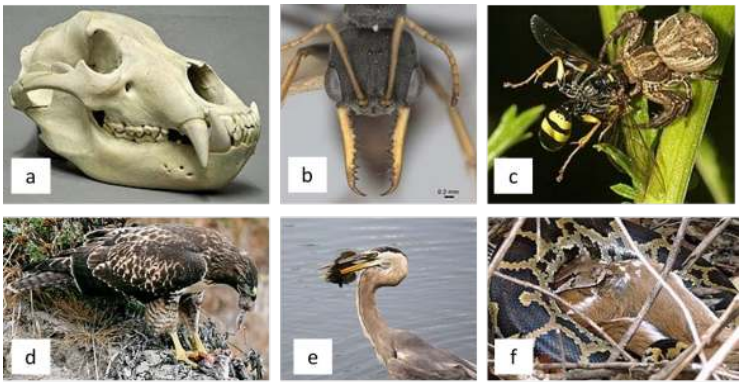


Figure 16.1.10: *a - Skull of brown bear has large pointed canines for killing prey, and self-sharpening carnassial teeth at rear for cutting flesh with a scissor-like action; b - Large compound eyes, sensitive antennae, and powerful jaws (mandibles) of jack jumper ant; c - Crab spider, an ambush predator with forward-facing eyes, catching another predator, a field digger wasp; d - Red-tailed hawk uses sharp hooked claws and beak to kill and tear up its prey; e - Specialist: a great blue heron with a speared fish; f - Indian python unhinges its jaw to swallow large prey like this chital*

Camouflage and mimicry

Camouflage is the use of any combination of materials, coloration, or illumination for concealment, either by making animals or objects hard to see, or by disguising them as something else. Predators may use camouflage to more effectively capture prey, while prey may use camouflage to more effectively evade predation. Members of the cat family such as the snow leopard (treeless highlands), tiger (grassy plains, reed swamps), ocelot (forest), fishing cat (waterside thickets), and lion (open plains) are camouflaged with coloration and disruptive patterns suiting their habitats (Figure 16.1.11).



Figure 16.1.11: *A camouflaged predator: snow leopard in Ladakh*

In aggressive mimicry, certain predators, including insects and fishes, make use of coloration and behavior to attract prey. Female *Photuris* fireflies, for example, copy the light signals of other species, thereby attracting male fireflies, which they capture and eat. Flower mantises are ambush predators; camouflaged as flowers, such as orchids, they attract prey and seize it when it is close enough. Frogfishes are extremely well camouflaged, and actively lure their prey to approach using an esca, a bait on the end of a rod-like appendage on the head, which they wave gently to mimic a small animal, gulping the prey in an extremely rapid movement when it is within range.



Figure 16.1.12: *Striated frogfish uses camouflage and aggressive mimicry in the form of a fishing rod-like lure on its head to attract prey.*

Other Adaptation Examples

- **Venom** - Many smaller predators such as the box jellyfish use venom to subdue their prey, and venom can also aid in digestion (as is the case for rattlesnakes and some spiders). The marbled sea snake that has adapted to egg predation has atrophied venom glands, and the gene for its three-finger toxin contains a mutation (the deletion of two nucleotides) that inactivates it. These changes are explained by the fact that its prey does not need to be subdued.
- **Electric fields** - Several groups of predatory fish have the ability to detect, track, and sometimes, as in the electric ray, incapacitate their prey by generating electric fields using electric organs. The electric organ is derived from modified nerve

or muscle tissue.

- **Physiology** - Physiological adaptations to predation include the ability of predatory bacteria to digest the complex peptidoglycan polymer from the cell walls of the bacteria that they prey upon. Carnivorous vertebrates of all five major classes (fishes, amphibians, reptiles, birds, and mammals) have lower relative rates of sugar to amino acid transport than either herbivores or omnivores, presumably because they acquire plenty of amino acids from the animal proteins in their diet.
- **Echolocation** - Echolocating animals emit calls out to the environment and listen to the echoes of those calls that return from various objects near them (Figure 16.1.13). They use these echoes to locate and identify the objects. Echolocation is used for navigation, foraging, and hunting in various environments.



Figure 16.1.13: *Bats use echolocation to hunt moths at night.*

Predator/Prey Coevolution

To counter predation, prey have evolved defenses for use at each stage of an attack. They can try to avoid detection, such as by using camouflage and mimicry. They can detect predators and warn others of their presence. If detected, they can try to avoid being the target of an attack, for example, by signaling that they are toxic or unpalatable, by forming groups, or that a chase would be unprofitable. If they become a target, they can try to fend off the attack with defenses such as armor, quills, unpalatability, or mobbing and they can escape an attack in progress by startling the predator, playing dead, shedding body parts such as tails, or simply fleeing.



Dead leaf mantis's camouflage makes it less visible to both predators and prey.



Syrphid hoverfly misdirects predators by mimicking a wasp, but has no sting.

Predators and prey are natural enemies, and many of their adaptations seem designed to counter each other. For example, bats have sophisticated echolocation systems to detect insects and other prey, and insects have developed a variety of defenses including the ability to hear echolocation calls. Many pursuit predators that run on land, such as wolves, have evolved long limbs in response to the increased speed of their prey. Their adaptations have been characterized as an **evolutionary arms race**, an example of the coevolution of two species. In a gene-centered view of evolution, the genes of predator and prey can be thought of as competing for the prey's body. Though criticized, the "life-dinner" principle of Dawkins and Krebs predicts that this arms race is asymmetric: if a predator fails to catch its prey, it loses its dinner, while if it succeeds, the prey loses its life.



Eastern coral snake, itself a predator, is venomous enough to kill predators that attack it, so when they avoid it, this behavior must be inherited, not learned.

The metaphor of an arms race implies ever-escalating advances in attack and defense. However, these adaptations come with a cost; for instance, longer legs have an increased risk of breaking, while the specialized tongue of the chameleon, with its ability to act like a projectile, is useless for lapping water, so the chameleon must drink dew off vegetation.

Consequences of Predation

Predators affect their ecosystems not only directly by eating their own prey, but by indirect means such as reducing predation by other species, or altering the foraging behavior of an herbivore, as with the biodiversity effect of wolves on riverside vegetation or sea otters on kelp forests. This may explain population dynamics effects such as the cycles observed in lynx and snowshoe hares.

Biodiversity maintained by apex predation

Predators may increase the biodiversity of communities by preventing a single species from becoming dominant. Such predators are known as keystone species and may have a profound influence on the balance of organisms in a particular ecosystem. Introduction or removal of this predator, or changes in its population density, can have drastic cascading effects on the equilibrium of many other populations in the ecosystem. For example, grazers of a grassland may prevent a single dominant species from taking over.



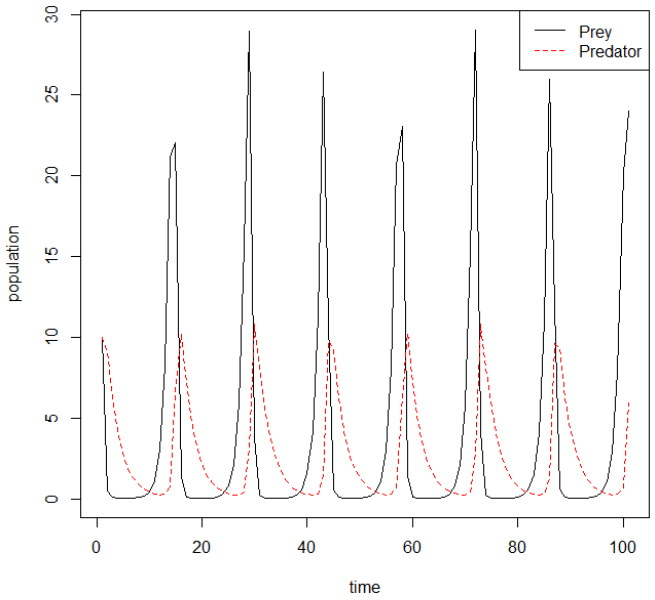
Riparian willow recovery at Blacktail Creek, Yellowstone National Park, after reintroduction of wolves, the local keystone species and apex predator. Left, in 2002; right, in 2015

The elimination of wolves from Yellowstone National Park had profound impacts on the entire ecosystem's structure and function. In Yellowstone, wolves are both keystone species and apex predators. Without predation, herbivores began to over-graze many woody browse species, affecting the area's plant populations. In addition, wolves often kept animals from grazing near streams, protecting the beavers' food sources. The removal of wolves had a direct effect on the beaver population, as their habitat became territory for grazing. Increased browsing on willows and conifers along Blacktail Creek due to a lack of predation caused channel incision because the reduced beaver population was no longer able to slow the water down and keep the soil in place. The predators were thus demonstrated to be of vital importance in the ecosystem.

Population dynamics

In the absence of predators, the population of a species can grow exponentially until it approaches the carrying capacity of the environment (Neal 2004). Predators limit the growth of prey both by consuming them and by changing their behavior. Increases or decreases in the prey population can also lead to increases or decreases in the number of predators, for example, through an increase in the number of young they bear.

Cyclical fluctuations have been seen in populations of predator and prey, often with offsets between the predator and prey cycles. A well-known example is that of the snowshoe hare and lynx. Over a broad span of boreal forests in Alaska and Canada, the hare populations fluctuate in near synchrony with a 10-year period, and the lynx populations fluctuate in response. This was first seen in historical records of animals caught by fur hunters for the Hudson Bay Company over more than a century.



Predator-prey population cycles in a Lotka-Volterra model

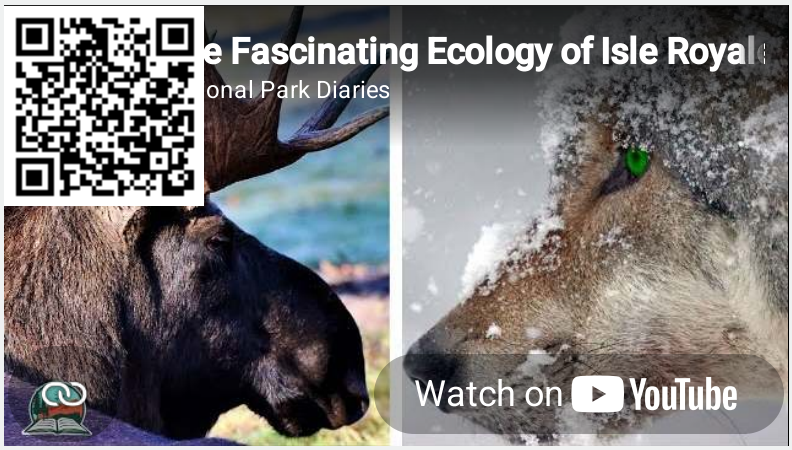
A simple model of a system with one species each of predator and prey, the Lotka–Volterra equations, predicts population cycles. However, attempts to reproduce the predictions of this model in the laboratory have often failed; for example, when the protozoan *Didinium nasutum* is added to a culture containing its prey, *Paramecium caudatum*, the latter is often driven to extinction.

The Lotka-Volterra equations rely on several simplifying assumptions, and they are structurally unstable, meaning that any change in the equations can stabilize or destabilize the dynamics. For example, one assumption is that predators have a linear functional response to prey: the rate of kills increases in proportion to the rate of encounters. If this rate is limited by time spent handling each catch, then prey populations can reach densities above which predators cannot control them. Another assumption is that all prey individuals are identical. In reality, predators tend to select young, weak, and ill individuals, leaving prey populations able to regrow.

Many factors can stabilize predator and prey populations. One example is the presence of multiple predators, particularly generalists that are attracted to a given prey species if it is abundant and look elsewhere if it is not. As a result, population cycles tend to be found in northern temperate and subarctic ecosystems because the food webs are simpler. The snowshoe hare-lynx system is subarctic, but even this involves other predators, including coyotes, goshawks and great horned owls, and the cycle is reinforced by variations in the food available to the hares.

A range of mathematical models have been developed by relaxing the assumptions made in the Lotka-Volterra model; these variously allow animals to have geographic distributions, or to migrate; to have differences between individuals, such as sexes and and age structure, so that only some individuals reproduce; to live in a varying environment, such as with changing seasons; and analyzing the interactions of more than just two species at once. Such models predict widely differing and often chaotic predator-prey population dynamics. The presence of refuge areas, where prey are safe from predators, may enable prey to maintain larger populations but may also destabilize the dynamics.

Video



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16.2: Quantifying Predator-Prey Dynamics

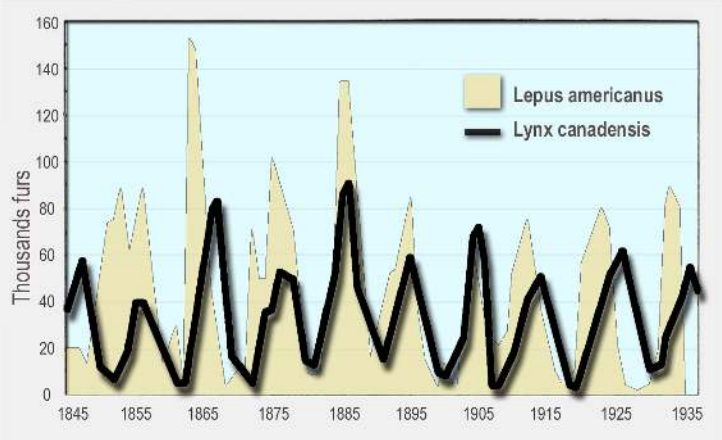


Figure 16.2.1**:** Numbers of snowshoe hare (*Lepus americanus*) (yellow background) and Canada lynx (black line, foreground) furs sold to the Hudson's Bay Company from 1845 to 1935. Image by Lamiot is licensed under CC BY-SA 4.0.

In the classic Lotka-Volterra model of predator-prey dynamics, both predators and prey are modeled using a modified version of the equation for exponential growth, so neither population has an explicit carrying capacity. However, either or both may have an implicit carrying capacity imposed by the interaction between the two populations.

To model the prey population, we begin with a basic exponential model with some additional terms. Here, the prey population is growing at their intrinsic growth rate r_{prey}, but is also declining due to predation.

The number of prey killed will depend on the number of predators: the greater the number of predators, the more prey they will kill (N_{pred}). It will also depend on the number of prey available: the more prey, the more successful the predators (N_{prey}). Finally, it will depend on the **attack rate**: the ability of a predator to find and consume prey (p). The number of prey killed in one time interval will be the product of these, $pN_{prey}N_{pred}$. The resulting equation for prey growth is:

$$\mathrm{dN_{prey}}/\mathrm{dt} = \mathrm{r_{prey}\,N_{prey}} - \mathrm{pN_{prey}\,N_{pred}}$$

In words, the prey population grows according to its per capita growth rate minus losses to predators. Losses are determined by attack rate, predator population, and prey population.

To model the predator population, we also begin with an exponential model, in concept. However, there is a wrinkle in this model, because we cannot assume a constant per capita rate of population growth. There is no simple *r* for the predator population because its growth rate will depend on how many prey are caught. As in the prey model, the number of prey caught will be $pN_{prey}N_{pred}$. The growth of the predator population will depend on this number, and on the efficiency with which predators convert consumed prey into predator offspring (*c* for conversion).

We will represent this conversion efficiency with the parameter *c*, so the per capita population growth of predators will be $cpN_{prey}N_{pred}$. We should reduce this predator population growth by some quantity to represent the starvation rate of predators who fail to consume prey. This will be the product of the per capita starvation rate times the predator population: dN_{pred}. Taking all this into account, we can write an equation for the predator population:

$$\mathrm{dN_{pred}}/\mathrm{dt} = \mathrm{cpN_{prey}\,N_{pred}} - \mathrm{d_{pred}\,N_{pred}}$$

In words, the predator population grows according to the attack rate, conversion efficiency, and prey population, minus losses to starvation.

Predator-Prey Model Parameters

dN_{prey}/dt = rate of change in prey population (change in number over change in time)

dN_{pred}/dt = rate of change in predator population (change in number over change in time)

c = rate at which prey are converted into offspring (a slope: predators produced per predator per time as a function of prey consumed per unit time)

p = attack rate efficiency (a slope: the change in prey consumed per predator per time as a function of the number of prey); higher search or handling time leads to a lower p

d_{pred} = predator death rate

r_{prey} = prey per capita rate of increase

N_{prey} = number of prey

N_{pred} = number of predators

It's important to note that the prey and predator equations above are **coupled equations**. In other words, the equation for prey includes a term for N_{pred} and the equation for predators includes the term N_{prey} and changes in one population will always impact the other population. Specifically, these equations lead to oscillations between the populations of predators and their prey.

We can ask several questions about the interaction between predators and their prey using these equations:

• Under what conditions (i.e., parameter values) will the predator population drive the prey to extinction?

• Under what conditions will the predator population die off, leaving the prey population to expand unhindered?

• Under what conditions will predator and prey populations both persist indefinitely? What will be their population dynamics while they coexist? In other words, will one or both populations stabilize, or will they continue to change over time?

Equilibrium Solutions

We will examine these questions by seeking equilibrium solutions to the coupled predator and prey equations we introduced above. For the prey population, we want to find values of predator and prey population sizes at which the prey population remains stable.

In other words, we want to solve for $dN_{pred}/dt = 0$ and $dN_{prey}/dt = 0$. Though we will not go through the derivations here, you can try them out on your own by replacing these terms with 0 then solving for N_{prey} and N_{pred}, respectively.

In words, the prey population reaches equilibrium when the predator population equals the prey's per capita growth rate divided by the predator's attack rate. Note that this is a constant. Strangely, the equilibrium size of the prey population is not determined by this solution, which says, in effect, that the prey population can be stable at any size as long as the predator population is at the specified size.

The isocline of Zero Growth for Prey occurs at $N_{pred} = r_{prey}/p$

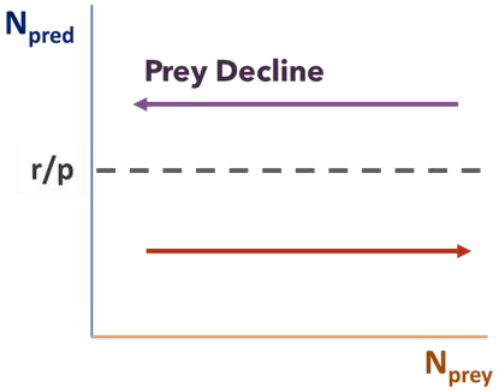


Figure 16.2.2**:** The dotted line (r/p) shows the isocline of zero growth for prey. They purple and orange lines show the direction of the prey and predator populations.

In words, the predator population reaches equilibrium when the prey population equals the predator's starvation rate over the product of attack rate times conversion efficiency. Note that this is also a constant, and like the solution for the prey population, it does not specify the equilibrium size of the predator population, only the size of the prey population at which the predators are at equilibrium.

The isocline of Zero Growth for Predator occurs at $N_{prey} = d/cp$

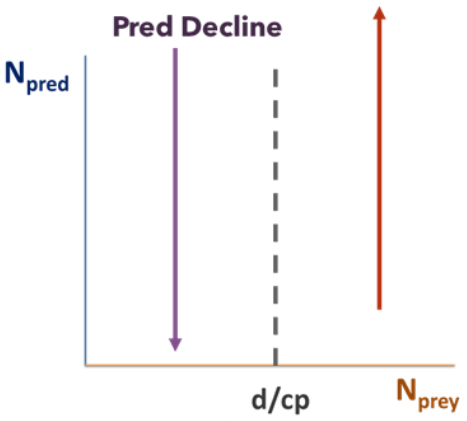


Figure 16.2.3**:** The dotted line shows the isocline of zero growth for predators (d/cp), while the purple and orange lines describe the direction the predator and prey populations will trend towards.

Now that we have solved for these isoclines, we can plot the population sizes of the two interacting populations on the two axes of a graph. The equilibrium solutions then become straight-line zero net growth isoclines (ZNGIs).

On this graph, the ZNGI for the prey population is a horizontal line at r_{prey}/p (orange line), below which the prey population increases, and above which it decreases. The ZNGI for the predator population is a vertical line at d/cp (blue line), to the left of which the predator population decreases, and to the right of which it increases (dashed arrows).

Where the two lines cross—at the point [d/cp, r_{prey}/p]—the two populations are at equilibrium. The continuous-time Lotka-Volterra model predicts that the point representing the two populations will cycle endlessly around the point where the two ZNGIs cross.

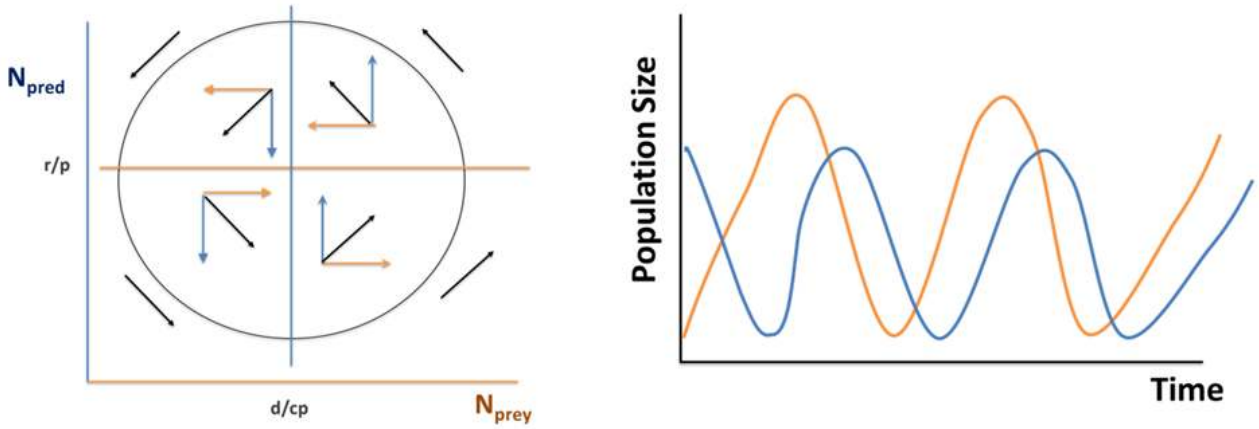


Figure 16.2.4**:** To the left, the isoclines for zero predator and prey growth are plotted. The vector arrows in each quadrant describe the counter-clockwise trends of the populations based on the movement from their initial populations to the point of equilibrium created by the isoclines. To the right, the boom-and-bust cycle of the populations are shown.

A Quick Summary - Coupled Predator-Prey Models

Based on the Exponential Model:

- Predators decline exponentially without food (prey)
- Prey increase exponentially without predation

Outcomes Depend on:

- Predator functional (p) and numerical (c) response
- Predator and prey birth/death rate
- Predator and prey initial population size

Steps for Finding the Oscillations:

- Find and plot d/cp
- Find and plot and r/p
- Plot initial population
- At isoclines, either predator or prey change trajectory

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16.3: Herbivory

Herbivory is a form of consumption in which an organism principally eats autotrophs (Abraham 2006) such as plants, algae and photosynthesizing bacteria. More generally, organisms that feed on autotrophs are known as **primary consumers.** Herbivory is usually limited to animals that eat plants. Fungi, bacteria, and protists that feed on living plants are usually termed plant pathogens (plant diseases), while fungi and microbes that feed on dead plants are described as saprotrophs. Flowering plants that obtain nutrition from other living plants are usually termed parasitic plants.

Feeding Strategies

Two herbivore feeding strategies are grazing (e.g. cows) and browsing (e.g. moose). For a terrestrial mammal to be called a grazer, at least 90% of the forage has to be grass, and for a browser at least 90% tree leaves and twigs. An intermediate feeding strategy is called "mixed-feeding" (Janis 1990) In their daily need to take up energy from forage, herbivores of different body mass may be selective in choosing their food. "Selective" means that herbivores may choose their forage source depending on, e.g., season or food availability, but also that they may choose high quality (and consequently highly nutritious) forage before lower quality. The latter especially is determined by the body mass of the herbivore, with small herbivores selecting for high-quality forage, and with increasing body mass animals are less selective.

Herbivores employ numerous types of feeding strategies. Many herbivores do not fall into one specific feeding strategy, but employ several strategies and eat a variety of plant parts.

Feeding Strategy	Diet	Example
Algivores	Algae	krill, crabs, sea snail, sea urchin, parrotfish, surgeonfish, flamingo
Frugivores	Fruit	Ruffed lemurs, orangutans
Folivores	Leaves	Koalas, gorillas, red colobuses
Nectarivores	Nectar	Honey possum, hummingbirds
Granivores	Seeds	Hawaiian honeycreepers
Graminivores	Grass	Horses
Palynivores	Pollen	Bees
Mucivores	Plant fluids, i.e. sap	Aphids
Xylophages	Wood	Termites

Plant-Herbivore Interactions

Interactions between plants and herbivores can play a prevalent role in ecosystem dynamics such community structure and functional processes. Plant diversity and distribution is often driven by herbivory, and it is likely that trade-offs between plant competitiveness and defensiveness, and between colonization and mortality allow for coexistence between species in the presence of herbivores. However, the effects of herbivory on plant diversity and richness is variable. For example, increased abundance of herbivores such as deer decrease plant diversity and species richness, while other large mammalian herbivores like bison control dominant species which allows other species to flourish. Plant-herbivore interactions can also operate so that plant communities mediate herbivore communities. Plant communities that are more diverse typically sustain greater herbivore richness by providing a greater and more diverse set of resources.

Coevolution and phylogenetic correlation between herbivores and plants are important aspects of the influence of herbivore and plant interactions on communities and ecosystem functioning, especially in regard to herbivorous insects. This is apparent in the adaptations plants develop to tolerate and/or defend from insect herbivory and the responses of herbivores to overcome these

adaptations. The evolution of antagonistic and mutualistic plant-herbivore interactions are not mutually exclusive and may co-occur. Plant phylogeny has been found to facilitate the colonization and community assembly of herbivores, and there is evidence of phylogenetic linkage between plant beta diversity and phylogenetic beta diversity of insect clades such as butterflies. These types of eco-evolutionary feedbacks between plants and herbivores are likely the main driving force behind plant and herbivore diversity.

Abiotic factors such as climate and biogeographical features also impact plant-herbivore communities and interactions. For example, in temperate freshwater wetlands herbivorous waterfowl communities change according to season, with species that eat above-ground vegetation being abundant during summer and species that forage below-ground being present in winter months. These seasonal herbivore communities differ in both their assemblage and functions within the wetland ecosystem. Such differences in herbivore modalities can potentially lead to trade-offs that influence species traits and may lead to additive effects on community composition and ecosystem functioning.

Seasonal changes and environmental gradients such as elevation and latitude often affect the palatability of plants which in turn influences herbivore community assemblages and vice versa. Examples include a decrease in abundance of leaf-chewing larvae in the fall when hardwood leaf palatability decreases due to increased tannin levels which results in a decline of arthropod species richness and increased palatability of plant communities at higher elevations where grasshoppers abundances are lower . Climatic stressors such as ocean acidification can lead to responses in plant-herbivore interactions in relation to palatability as well .

Herbivore Offense

The myriad defenses displayed by plants means that their herbivores need a variety of skills to overcome these defenses and obtain food. These allow herbivores to increase their feeding and use of a host plant. Herbivores have three primary strategies for dealing with plant defenses: choice, herbivore modification, and plant modification.

Feeding choice involves which plants a herbivore chooses to consume. It has been suggested that many herbivores feed on a variety of plants to balance their nutrient uptake and to avoid consuming too much of any one type of defensive chemical. This involves a tradeoff however, between foraging on many plant species to avoid toxins or specializing on one type of plant that can be detoxified.

Herbivore modification is when various adaptations to body or digestive systems of the herbivore allow them to overcome plant defenses. This might include detoxifying secondary metabolites, sequestering toxins unaltered, or avoiding toxins, such as through the production of large amounts of saliva to reduce the effectiveness of defenses. Herbivores may also utilize symbionts to evade plant defenses. For example, some aphids use bacteria in their gut to provide essential amino acids lacking in their sap diet.



Figure 16.3.1: *Aphids are fluid feeders on plant sap.*

Plant modification occurs when herbivores manipulate their plant prey to increase feeding. For example, some caterpillars roll leaves to reduce the effectiveness of plant defenses activated by sunlight.

Plant Defense

A **plant defense** is a trait that increases plant fitness when faced with herbivory. This is measured relative to another plant that lacks the defensive trait. Plant defenses increase the survival and/or reproduction (fitness) of plants under the pressure of predation

from herbivores.

Defense can be divided into two main categories, tolerance and resistance. Tolerance is the ability of a plant to withstand damage without a reduction in fitness. This can occur by diverting herbivory to non-essential plant parts, resource allocation, compensatory growth, or by rapid regrowth and recovery from herbivory. Resistance refers to the ability of a plant to reduce the amount of damage it receives from herbivores. This can occur via avoidance in space or time, physical defenses, or chemical defenses. Defenses can either be constitutive, always present in the plant, or induced, produced or translocated by the plant following damage or stress.

Physical, or mechanical, defenses are barriers or structures designed to deter herbivores or reduce intake rates, lowering overall herbivory. Thorns such as those found on roses or acacia trees are one example, as are the spines on a cactus. Smaller hairs known as trichomes may cover leaves or stems and are especially effective against invertebrate herbivores. In addition, some plants have waxes or resins that alter their texture, making them difficult to eat. Also the incorporation of silica into cell walls is analogous to that of the role of lignin in that it is a compression-resistant structural component of cell walls; so that plants with their cell walls impregnated with silica are thereby afforded a measure of protection against herbivory.

Chemical defenses are secondary metabolites produced by the plant that deter herbivory. There are a variety of these in nature and a single plant can have hundreds of different chemical defenses. Chemical defenses can be divided into two main groups, carbon-based defenses and nitrogen-based defenses.

1. Carbon-based defenses include terpenes and phenolics. Terpenes are derived from 5-carbon isoprene units and comprise essential oils, carotenoids, resins, and latex. They can have several functions that disrupt herbivores such as inhibiting adenosine triphosphate (ATP) formation, molting hormones, or the nervous system. Phenolics combine an aromatic carbon ring with a hydroxyl group. There are several different phenolics such as lignins, which are found in cell walls and are very indigestible except for specialized microorganisms; tannins, which have a bitter taste and bind to proteins making them indigestible; and furanocumerins, which produce free radicals disrupting DNA, protein, and lipids, and can cause skin irritation.
2. Nitrogen-based defenses are synthesized from amino acids and primarily come in the form of alkaloids and cyanogens. Alkaloids include commonly recognized substances such as caffeine, nicotine, and morphine. These compounds are often bitter and can inhibit DNA or RNA synthesis or block nervous system signal transmission. Cyanogens get their name from the cyanide stored within their tissues. This is released when the plant is damaged and inhibits cellular respiration and electron transport.

Plants have also changed features that enhance the probability of attracting natural enemies to herbivores. Some emit semiochemicals, odors that attract natural enemies, while others provide food and housing to maintain the natural enemies' presence, e.g. ants that reduce herbivory. A given plant species often has many types of defensive mechanisms, mechanical or chemical, constitutive or induced, which allow it to escape from herbivores.

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16.4: Pathogens

An **infection** is the invasion of an organism's body tissues by disease-causing agents, their multiplication, and the reaction of host tissues to the infectious agents and the toxins they produce. An **infectious disease**, also known as **transmissible disease** or **communicable disease**, is an illness resulting from an infection.

Infections can be caused by a wide range of pathogens, most prominently bacteria and viruses. Hosts can fight infections using their immune systems. Mammalian hosts react to infections with an innate response, often involving inflammation, followed by an adaptive response.

Pathophysiology

There is a general chain of events that applies to infections, sometimes called the **chain of infection** (Figure 16.4.1). The chain of events involves several steps – which include the infectious agent, reservoir, entering a susceptible host, exit, and transmission to new hosts. Each of the links must be present in chronological order for an infection to develop. Understanding these steps helps healthcare workers target the infection and prevent it from occurring in the first place.

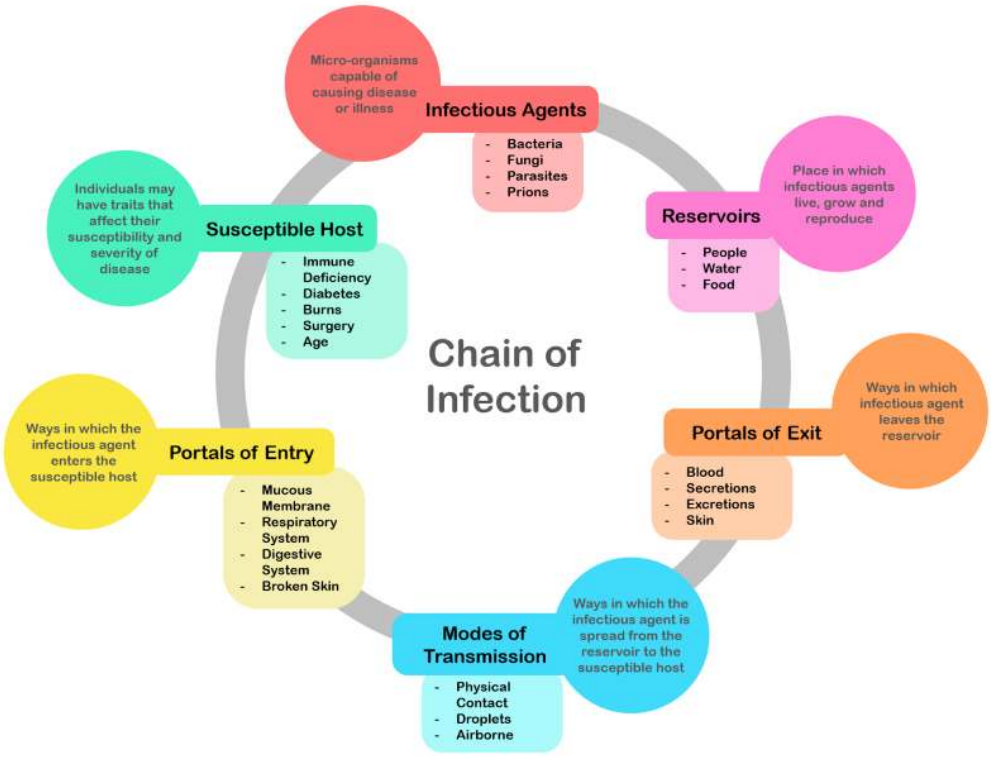


Figure 16.4.1: *Chain of infection; the chain of events that lead to infection*

Colonization

Infection begins when an organism successfully enters the body, grows, and multiplies. This is referred to as **colonization**. Individuals with compromised or weakened immune systems have an increased susceptibility to chronic or persistent infections. Individuals who have a suppressed immune system are particularly susceptible to opportunistic infections. Entrance to the host at host-pathogen interface generally occurs through the mucosa in orifices like the oral cavity, nose, eyes, genitalia, anus, or the microbe can enter through open wounds. While a few organisms can grow at the initial site of entry, many migrate and cause systemic infection in different organs. Some pathogens grow within the host cells (intracellular) whereas others grow freely in bodily fluids (Figure 16.4.2).

Wound colonization refers to non-replicating microorganisms within the wound, while in infected wounds, replicating organisms exist and tissue is injured. All multicellular organisms are colonized to some degree by extrinsic organisms, and the vast majority of these exist in either a mutualistic or commensal relationship with the host. An example of the former is the anaerobic bacteria

species, which colonizes the mammalian colon, and an example of the latter are the various species of staphylococcus that exist on human skin. Neither of these colonizations are considered infections.

The difference between an infection and a colonization is often only a matter of circumstance. Non-pathogenic organisms can become pathogenic given specific conditions, and even the most virulent organism requires certain circumstances to cause a compromising infection. Some colonizing bacteria, such as *Corynebacteria sp.* and *viridans streptococci*, prevent the adhesion and colonization of pathogenic bacteria and thus have a symbiotic relationship with the host, preventing infection and speeding wound healing.

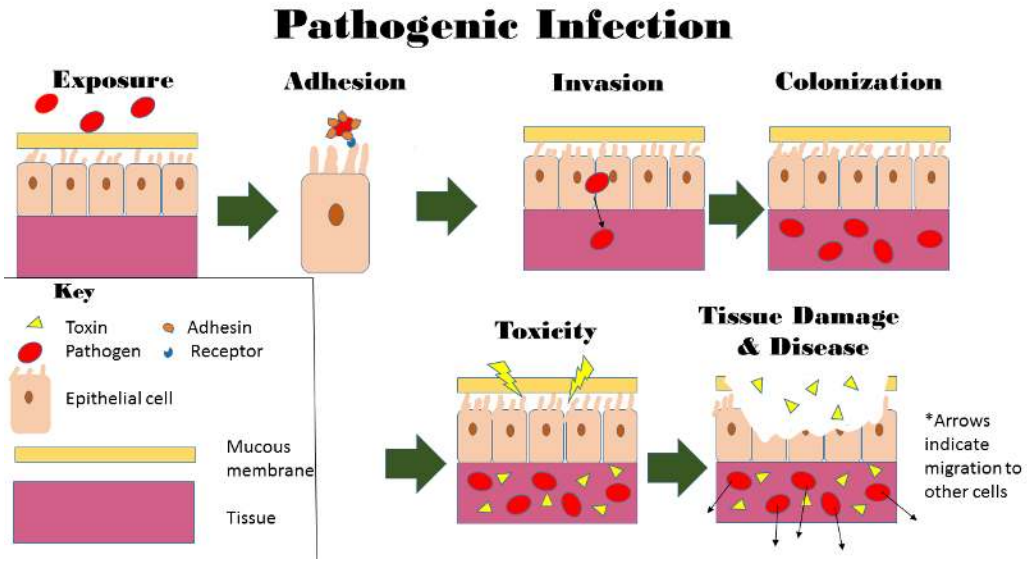


Figure 16.4.2: *This image depicts the steps of pathogenic infection.*

The variables involved in the outcome of a host becoming inoculated by a pathogen and the ultimate outcome include:

- the route of entry of the pathogen and the access to host regions that it gains
- the intrinsic virulence of the particular organism
- the quantity or load of the initial inoculant
- the immune status of the host being colonized

As an example, several staphylococcal species remain harmless on the skin, but, when present in a normally sterile space, such as in the capsule of a joint or the peritoneum, multiply without resistance and cause harm.

Disease

Disease can arise if the host's protective immune mechanisms are compromised and the organism inflicts damage on the host. Microorganisms can cause tissue damage by releasing a variety of toxins or destructive enzymes. For example, *Clostridium tetani* releases a toxin that paralyzes muscles, and staphylococcus releases toxins that produce shock and sepsis. Not all infectious agents cause disease in all hosts. For example, less than 5% of individuals infected with polio develop disease. On the other hand, some infectious agents are highly virulent. The prion-causing mad cow disease and Creutzfeldt–Jakob disease invariably kill all animals and people that are infected.

Persistent infections occur because the body is unable to clear the organism after the initial infection. Persistent infections are characterized by the continual presence of the infectious organism, often as latent infection with occasional recurrent relapses of active infection. There are some viruses that can maintain a persistent infection by infecting different cells of the body. Some viruses once acquired never leave the body. A typical example is the herpes virus, which tends to hide in nerves and become reactivated when specific circumstances arise.

Transmission

For infecting organisms to survive and repeat the infection cycle in other hosts, they (or their progeny) must leave an existing reservoir and cause infection elsewhere. The relationship between *virulence versus transmissibility* is complex; if a disease is rapidly fatal, the host may die before the microbe can be passed along to another host. Infection transmission can take place via many potential routes:

- **Droplet contact**, also known as the *respiratory route*, and the resultant infection can be termed airborne disease. If an infected individual coughs or sneezes on another individual the microorganisms, suspended in warm, moist droplets, may enter the body through the nose, mouth or eye surfaces.
- **Fecal-oral transmission**, wherein food or water become contaminated and individuals who eat and drink them become infected. Common fecal-oral transmitted pathogens include *Vibrio cholerae*, *Giardia* species, rotaviruses, *Entameba histolytica*, *Escherichia coli*, and tapeworms. Most of these pathogens cause gastroenteritis.
- **Sexual transmission**, with the resulting disease being called sexually transmitted disease
- **Oral transmission**, diseases that are transmitted primarily by oral means may be caught through direct or indirect oral contact between individuals.
- **Transmission by direct contact**, Some diseases that are transmissible by direct contact include athlete's foot, impetigo and warts.
- **Vehicle transmission,** transmission by an inanimate reservoir (food, water, soil)
- **Vertical transmission**, directly from the mother to an embryo, fetus or offspring during pregnancy or birth. It can occur as a result of a pre-existing infection or one acquired during pregnancy.
- **Latrogenic transmission**, due to medical procedures such as injection or transplantation of infected material.
- **Vector-borne transmission**, transmitted by a vector, which is an organism that does not cause disease itself but that transmits infection by conveying pathogens from one host to another (Figure 16.4.3).



Figure 16.4.3: *A southern house mosquito (Culex quinquefasciatus) is a vector that transmits the pathogens that cause West Nile fever and avian malaria among others.*

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CHAPTER OVERVIEW

Chapter 17: Symbioses

Learning Objectives

- Introduce and explore the types of mutualisms, parasitisms, commensalisms
- Explore theories that explain the evolution of mutualisms
- Discuss hypotheses regarding the maintenance of mutualistic relationships

Video



17.1: Introduction to Symbioses
17.1: Parasitism
17.2: Mutualisms
17.4: Maintenance of Mutualisms
17.5: Commensalisms

Summary

A commensal relationship occurs when one species benefits from a close prolonged interaction, while the other neither benefits nor is harmed. A mutualism occurs when two species benefit from their interaction, and can be generalized into three types: resource-resource, service-resource, and service-service. Many mutualisms are thought to have evolved from antagonistic interactions, such as parasite-host relationships.

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17.1: Introduction to Symbioses

Commensalism

A commensal relationship occurs when one species benefits from a close prolonged interaction, while the other neither benefits nor is harmed. Birds nesting in trees provide an example of a commensal relationship (Figure 17.1.1). The tree is not harmed by the presence of the nest among its branches. The nests are light and produce little strain on the structural integrity of the branch, and most of the leaves, which the tree uses to get energy by photosynthesis, are above the nest so they are unaffected. The bird, on the other hand, benefits greatly. If the bird had to nest in the open, its eggs and young would be vulnerable to predators. Many potential commensal relationships are difficult to identify because it is difficult to prove that one partner does not derive some benefit from the presence of the other.



Figure 17.1.1**:** The southern masked-weaver is starting to make a nest in a tree in Zambezi Valley, Zambia. This is an example of a commensal relationship, in which one species (the bird) benefits, while the other (the tree) neither benefits nor is harmed. (credit: "Hanay"/Wikimedia Commons)

Mutualism

A mutualism occurs when two species benefit from their interaction. For example, termites have a mutualistic relationship with protists that live in the insect's gut (Figure 17.1.2**a**). The termite benefits from the ability of the protists to digest cellulose. However, the protists are able to digest cellulose only because of the presence of symbiotic bacteria within their cells that produce the cellulase enzyme. The termite itself cannot do this: without the protozoa, it would not be able to obtain energy from its food (cellulose from the wood it chews and eats). The protozoa benefit by having a protective environment and a constant supply of food from the wood chewing actions of the termite. In turn, the protists benefit from the enzymes provided by their bacterial endosymbionts, while the bacteria benefit from a doubly protective environment and a constant source of nutrients from two hosts. Lichen are a mutualistic relationship between a fungus and photosynthetic algae or cyanobacteria (Figure 17.1.2**b**). The glucose produced by the algae provides nourishment for both organisms, whereas the physical structure of the lichen protects the algae from the elements and makes certain nutrients in the atmosphere more available to the algae. The algae of lichens can live independently given the right environment, but many of the fungal partners are unable to live on their own.



(a) (b)

Figure 17.1.2**:** (a) Termites form a mutualistic relationship with symbiotic protozoa in their guts, which allow both organisms to obtain energy from the cellulose the termite consumes. (b) Lichen is a fungus that has symbiotic photosynthetic algae living in close association. (credit a: modification of work by Scott Bauer, USDA; credit b: modification of work by Cory Zanker)

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17.1: Parasitism



A fish parasite, the isopod Cymothoa exigua, replacing the tongue of a Lithognathus

Parasitism is a close relationship between species, where one organism, the parasite, lives on or inside another organism, the host, causing it some harm, and is adapted structurally to this way of life (Poulin 2007). Like predation, parasitism is a type of consumer-resource interaction (Getz 2011), but unlike predators, parasites, with the exception of parasitoids, are typically much smaller than their hosts, do not kill them, and often live in or on their hosts for an extended period. Parasites of animals are highly specialized, and reproduce at a faster rate than their hosts. Classic examples include interactions between vertebrate hosts and tapeworms, flukes, the malaria-causing *Plasmodium* species, and fleas.

Parasites reduce host fitness by general or specialized pathology, from parasitic castration to modification of host behavior. Parasites increase their own fitness by exploiting hosts for resources necessary for their survival, in particular by feeding on them and by using intermediate (secondary) hosts to assist in their transmission from one definitive (primary) host to another. Although parasitism is often unambiguous, it is part of a spectrum of interactions between species, grading via parasitoidism into predation, through evolution into mutualism, and in some fungi, shading into being saprophytic.

Within that scope are many possible strategies. Taxonomists classify parasites in a variety of overlapping schemes, based on their interactions with their hosts and on their life-cycles, which are sometimes very complex. An **obligate** parasite depends completely on the host to complete its life cycle, while a **facultative** parasite does no. Parasite life-cycles involving only one host are called **"direct"**; those with a definitive host (where the parasite reproduces sexually) and at least one intermediate host are called **"indirect"** (Garcia 1999). An **endoparasite** lives inside the host's body; an **ectoparasite** lives outside, on the host's surface (Australian Society of Parasitology 2010). **Mesoparasites**—like some copepods, for example—enter an opening in the host's body and remain partly embedded there (Vecchione and Aznar 2008). Some parasites can be generalists, feeding on a wide range of hosts, but many parasites, and the majority of protozoans and helminths that parasitise animals, are specialists and extremely host-specific (Australian Society of Parasitology 2010). The microorganisms and viruses that can reproduce and complete their life cycle within the host are known as **microparasites**. **Macroparasites** are the multicellular organisms that reproduce and complete their life cycle outside of the host or on the host's body (Poulin 2011; Blackwell Science 2018).

Strategies

There are six major parasitic strategies, namely parasitic castration; directly transmitted parasitism; trophically-transmitted parasitism; vector-transmitted parasitism; parasitoidism; and micropredation. These apply to parasites whose hosts are plants as well as animals (Poulin 2011; Poulin 2015). These strategies represent adaptive peaks; intermediate strategies are possible, but organisms in many different groups have consistently converged on these six, which are evolutionarily stable (Poulin 2011).

A perspective on the evolutionary options can be gained by considering four key questions: the effect on the fitness of a parasite's hosts; the number of hosts they have per life stage; whether the host is prevented from reproducing; and whether the effect depends on intensity (number of parasites per host). From this analysis, the major evolutionary strategies of parasitism emerge, alongside predation (Lafferty and Kuris 2002).

Host fitness	**Single host, stays alive**	**Single host, dies**	**Multiple hosts**
Able to reproduce (fitness > 0)	Conventional parasite *Pathogen*	Trophically-transmitted parasite *Trophically-transmitted pathogen*	Micropredator *Micropredator*
Unable to reproduce (fitness = 0)	----- *Parasitic castrator*	Trophically-transmitted parasitic castrator *Parasitoid*	Social predator *Solitary predator*

Parasitic castrators



The parasitic castrator Sacculina carcini (highlighted) attached to its crab host

Parasitic castrators partly or completely destroy their host's ability to reproduce, diverting the energy that would have gone into reproduction into host and parasite growth, sometimes causing gigantism in the host. The host's other systems remain intact, allowing it to survive and to sustain the parasite (Poulin 2015; Poulin 2007). Parasitic crustaceans such as those in the specialized barnacle genus *Sacculina* specifically cause damage to the gonads of their many species (Elumalai et al. 2013) of host crabs. In the case of *Sacculina*, the testes of over two-thirds of their crab hosts degenerate sufficiently for these male crabs to develop female secondary sex characteristics such as broader abdomens, smaller claws and egg-grasping appendages. Various species of helminth castrate their hosts (such as insects and snails). This may happen directly, whether mechanically by feeding on their gonads, or by secreting a chemical that destroys reproductive cells; or indirectly, whether by secreting a hormone or by diverting nutrients. For example, the trematode *Zoogonus lasius*, whose sporocysts lack mouths, castrates the intertidal marine snail *Tritia obsoleta* chemically, developing in its gonad and killing its reproductive cells (Poulin 2007; Cheng 2012).

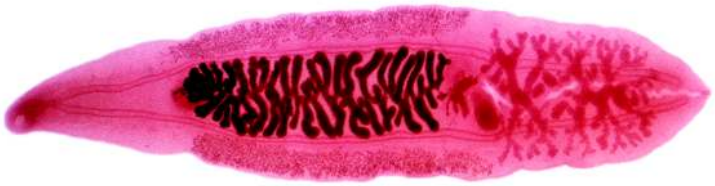
Directly-Transmitted



Human head-lice exemplify directly transmitted obligate ectoparasites

Directly-transmitted parasites, not requiring a vector to reach their hosts, include such parasites of terrestrial vertebrates as lice and mites; marine parasites such as copepods and cyamid amphipods; monogeneans; and many species of nematodes, fungi, protozoans, bacteria, and viruses. Whether endoparasites or ectoparasites, each has a single host-species. Within that species, most individuals are free or almost free of parasites, while a minority carry a large number of parasites; this is known as an aggregated distribution (Poulin 2015).

Trophically-transmitted



Clonorchis sinensis, the Chinese liver fluke, is trophically transmitted

Trophically-transmitted parasites are transmitted by being eaten by a host. They include trematodes (all except schistosomes), cestodes, acanthocephalans, pentastomids, many round worms, and many protozoa such as *Toxoplasma* (Poulin 2015). They have complex life-cycles involving hosts of two or more species. In their juvenile stages they infect and often encyst in the intermediate host. When the intermediate-host animal is eaten by a predator, the definitive host, the parasite survives the digestion process and matures into an adult; some live as intestinal parasites. Many trophically-transmitted parasites modify the behavior of their intermediate hosts, increasing their chances of being eaten by a predator. As with directly transmitted parasites, the distribution of trophically transmitted parasites among host individuals is aggregated (Poulin 2015). Coinfection by multiple parasites is common (Cox 2001). Autoinfection, where (by exception) the whole of the parasite's life-cycle takes place in a single primary host, can sometimes occur in helminths such as *Strongyloides stercoralis* (Australian Society of Parasitology 2017).

Vector-transmitted



The vector-transmitted protozoan endoparasite Trypanosoma among human red blood cells

Vector-transmitted parasites rely on a third party, an intermediate host, where the parasite does not reproduce sexually (Australian Society of Parasitology 2010) to carry them from one definitive host to another (Poulin and Randhawa 2015). These parasites are microorganisms, namely protozoa, bacteria, or viruses, often intracellular pathogens (disease-causers) (Poulin and Randhawa 2015). Their vectors are mostly hematophagic arthropods such as fleas, lice, ticks, and mosquitoes (Poulin and Randhawa 2015, PEOI 2013). For example, the deer tick *Ixodes scapularis* acts as a vector for diseases including Lyme disease, babesiosis, and anaplasmosis (Steere 2001). Protozoan endoparasites, such as the malarial parasites in the genus *Plasmodium* and sleeping-sickness parasites in the genus *Trypanosoma*, have infective stages in the host's blood which are transported to new hosts by biting insects (Pollitt et al. 2011).

Parasitoids

Parasitoids are insects which sooner or later kill their hosts, placing their relationship close to predation (Stevens 2010). Most parasitoids are parasitoid wasps or other hymenopterans; others include dipterans such as phorid flies. They can be divided into two groups, idiobionts and koinobionts, differing in their treatment of their hosts (Gullan and Cranston 2010).

Idiobiont parasitoids sting their often large prey on capture, either killing them outright or paralyzing them immediately. The immobilized prey is then carried to a nest, sometimes alongside other prey if it is not large enough to support a parasitoid throughout its development. An egg is laid on top of the prey and the nest is then sealed. The parasitoid develops rapidly through its larval and pupal stages, feeding on the provisions left for it (Gullan and Cranston 2010).



Idiobiont parasitoid wasps immediately paralyze their hosts for their larvae (Pimplinae, pictured) to eat (Poulin and Randhawa 2015).

Koinobiont parasitoids, which include flies as well as wasps, lay their eggs inside young hosts, usually larvae. These are allowed to go on growing, so the host and parasitoid develop together for an extended period, ending when the parasitoids emerge as adults, leaving the prey dead, eaten from inside. Some koinobionts regulate their host's development, for example preventing it from pupating or making it molt whenever the parasitoid is ready to molt. They may do this by producing hormones that mimic the host's molting hormones (ecdysteroids), or by regulating the host's endocrine system (Gullan and Cranston 2010).



Koinobiont parasitoid wasps like this braconid lay their eggs inside their hosts, which continue to grow and moult.



Phorid fly (center left) is laying eggs in the abdomen of a worker honey-bee, altering its behavior.

Micropredators



Mosquitoes are micropredators, and important vectors of disease

A micropredator attacks more than one host, reducing each host's fitness by at least a small amount, and is only in contact with any one host intermittently. This behavior makes micropredators suitable as vectors, as they can pass smaller parasites from one host to another (Poulin and Randhawa 2015; Lafferty and Kuris 2002; Wilson et al. 2017). Most micropredators are hematophagic, feeding on blood. They include annelids such as leeches, crustaceans such as branchiurans and gnathiid isopods, various dipterans such as mosquitoes and tsetse flies, other arthropods such as fleas and ticks, vertebrates such as lampreys, and mammals such as vampire bats (Poulin and Randhawa 2015).

Variations on Parasitism

Hyperparasitism

Hyperparasites feed on another parasite, as exemplified by protozoa living in helminth parasites (Dissanaike 1957), or facultative or obligate parasitoids whose hosts are either conventional parasites or parasitoids (Poulin and Randhawa 2015; Gullan and Cranston 2010). Levels of parasitism beyond secondary also occur, especially among facultative parasitoids. In oak gall systems, there can be up to five levels of parasitism (Askew 1951).

Hyperparasites can control their hosts' populations, and are used for this purpose in agriculture and to some extent in medicine. The controlling effects can be seen in the way that the CHV1 virus helps to control the damage that chestnut blight, *Cryphonectria parasitica*, does to American chestnut trees, and in the way that bacteriophages can limit bacterial infections. It is likely, though little researched, that most pathogenic microparasites have hyperparasites which may prove widely useful in both agriculture and medicine (Parratt and Laine 2016).



A hyperparasitoid pteromalid wasp on the cocoons of its host, itself a parasitoid braconid wasp

Social parasitism

Social parasites take advantage of interspecific interactions between members of eusocial animals such as ants, termites, and bumblebees. Examples include the large blue butterfly, *Phengaris arion*, its larvae employing ant mimicry to parasitise certain ants (Thomas et al. 2010), *Bombus bohemicus*, a bumblebee which invades the hives of other bees and takes over reproduction while their young are raised by host workers, and *Melipona scutellaris*, a eusocial bee whose virgin queens escape killer workers and invade another colony without a queen (Van Oystaeyen et al. 2013) An extreme example of interspecific social parasitism is found in the ant *Tetramorium inquilinum*, an obligate parasite which lives exclusively on the backs of other *Tetramorium* ants (Antkeepers 2016).



The large blue butterfly is an ant mimic and social parasite.

Brood parasitism

In brood parasitism, the hosts act as parents as they raise the young as their own. Brood parasites include birds in different families such as cowbirds, whydahs, cuckoos, and black-headed ducks. These do not build nests of their own, but leave their eggs in nests of other species. The eggs of some brood parasites mimic those of their hosts, while some cowbird eggs have tough shells, making them hard for the hosts to kill by piercing, both mechanisms implying selection by the hosts against parasitic eggs (Payne 1997;

Rothstein 1990; De Marsico et al. 2013). The adult female European cuckoo further mimics a predator, the European sparrowhawk, giving her time to lay her eggs in the host's nest unobserved (Welbergen and Davies 2011).



In brood parasitism, the host raises the young of another species, here a cowbird's egg, that has been laid in its nest.

Kleptoparasitism

In kleptoparasitism (from Greek κλέπτης (*kleptēs*), "thief"), parasites steal food gathered by the host. The parasitism is often on close relatives, whether within the same species or between species in the same genus or family. For instance, the many lineages of cuckoo bees lay their eggs in the nest cells of other bees in the same family (Slater et al. 2005). Kleptoparasitism is uncommon generally but conspicuous in birds; some such as skuas are specialized in pirating food from other seabirds, relentlessly chasing them down until they disgorge their catch (Furness 1978).



The great skua is a powerful kleptoparasite, relentlessly pursuing other seabirds until they disgorge their catches of food.

Sexual parasitism

A unique approach is seen in some species of anglerfish, such as *Ceratias holboelli*, where the males are reduced to tiny sexual parasites, wholly dependent on females of their own species for survival, permanently attached below the female's body, and unable to fend for themselves. The female nourishes the male and protects him from predators, while the male gives nothing back except the sperm that the female needs to produce the next generation (Pietsch 2005).



The male anglerfish Ceratias holboelli lives as a tiny sexual parasite permanently attached below the female's body.

Adelphoparasitism

Adelphoparasitism, (from Greek ἀδελφός (*adelphós*), brother – Maggenti et al. 2005), also known as sibling-parasitism, occurs where the host species is closely related to the parasite, often in the same family or genus (Rochat and Gutierrez 2001). In the citrus blackfly parasitoid, *Encarsia perplexa*, unmated females of which may lay haploid eggs in the fully developed larvae of their own species, producing male offspring (University of Florida 2018), while the marine worm *Bonellia viridis* has a similar reproductive strategy, although the larvae are planktonic (Berec et al. 2005).



Encarsia perplexa (center), a parasitoid of citrus blackfly (lower left), is also an adelphoparasite, laying eggs in larvae of its own species

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17.2: Mutualisms

Introduction to Mutualisms

Mutualism

A mutualism occurs when two species benefit from their interaction. For example, termites have a mutualistic relationship with protists that live in the insect's gut (Figure 17.2.2**a**). The termite benefits from the ability of the protists to digest cellulose. However, the protists are able to digest cellulose only because of the presence of symbiotic bacteria within their cells that produce the cellulase enzyme. The termite itself cannot do this: without the protozoa, it would not be able to obtain energy from its food (cellulose from the wood it chews and eats). The protozoa benefit by having a protective environment and a constant supply of food from the wood-chewing actions of the termite. In turn, the protists benefit from the enzymes provided by their bacterial endosymbionts, while the bacteria benefit from a doubly protective environment and a constant source of nutrients from two hosts.

Lichen are a mutualistic relationship between a fungus and photosynthetic algae or cyanobacteria (Figure 17.2.2**b**). The glucose produced by the algae provides nourishment for both organisms, whereas the physical structure of the lichen protects the algae from the elements and makes certain nutrients in the atmosphere more available to the algae. The algae of lichens can live independently given the right environment, but many of the fungal partners are unable to live on their own.



(a) (b)

Figure 17.2.1: (a) Termites form a mutualistic relationship with symbiotic protozoa in their guts, which allow both organisms to obtain energy from the cellulose the termite consumes. (b) Lichen is a fungus that has symbiotic photosynthetic algae living in close association. (credit a: modification of work by Scott Bauer, USDA; credit b: modification of work by Cory Zanker)

Types of Mutualisms

Resource-resource relationships

Mutualistic relationships can be thought of as a form of "biological barter" in mycorrhizal associations between plant roots and fungi, with the plant providing carbohydrates to the fungus in return for primarily phosphate but also nitrogenous compounds. Other examples include rhizobia bacteria that fix nitrogen for leguminous plants (family Fabaceae) in return for energy-containing carbohydrates.

Service-resource relationships

Figure 17.2.2: The red-billed oxpecker eats ticks on the impala's coat, in a cleaning symbiosis. Photograph by Muhammad Mahdi Karim.

Service-resource relationships are common. Three important types are pollination, cleaning symbiosis, and zoochory. In pollination, a plant trades food resources in the form of nectar or pollen for the service of pollen dispersal. Phagophiles feed (resource) on ectoparasites, thereby providing anti-pest service, as in cleaning symbiosis ()Figure 17.2.2. *Elacatinus* and *Gobiosoma*, genera of gobies, feed on ectoparasites of their clients while cleaning them and zoochory is the dispersal of the seeds of plants by animals. This is similar to pollination in that the plant produces food resources (for example, fleshy fruit,

overabundance of seeds) for animals that disperse the seeds (service). Plants may advertise these resources using color and a variety of other fruit characteristics. Another type is ant protection of aphids, where the aphids trade sugar-rich honeydew (a by-product of their mode of feeding on plant sap) in return for defense against predators such as ladybugs.

Service-service relationships



Figure 17.2.3: Ocellaris clownfish and Ritter's sea anemones live in a mutual service-service symbiosis, the fish driving off butterflyfish and the anemone's tentacles protecting the fish from predators. Photograph by Jan Derk in the Public Domain.

Strict service-service interactions are very rare, for reasons that are far from clear. One example is the relationship between sea anemones and anemone fish in the family Pomacentridae: the anemones provide the fish with protection from predators (which cannot tolerate the stings of the anemone's tentacles) and the fish defend the anemones against butterflyfish (family Chaetodontidae), which eat anemones (Figure 17.2.3. However, in common with many mutualisms, there is more than one aspect to it: in the anemonefish-anemone mutualism, waste ammonia from the fish feeds the symbiotic algae that are found in the anemone's tentacles. Therefore, what appears to be a service-service mutualism in fact has a service-resource component.

A second example is that of the relationship between some ants in the genus *Pseudomyrmex* and trees in the genus *Acacia*, such as the whistling thorn and bullhorn acacia. The ants nest inside the plant's thorns. In exchange for shelter, the ants protect acacias from attack by herbivores (which they frequently eat when those are small enough, introducing a resource component to this service-service relationship) and competition from other plants by trimming back vegetation that would shade the acacia. In addition, another service-resource component is present, as the ants regularly feed on lipid-rich food-bodies called Beltian bodies that are on the *Acacia* plant.

Evolution of Mutualisms

Many mutualisms are thought to have evolved from antagonistic interactions. Several studies have determined ecological or evolutionary conditions driving transitions from mutualism to antagonism (mutualism breakdown), yet limited theory has been developed to mechanistically explain the evolutionary transitions from antagonism to mutualism. Models of virulence predict evolution of reduced antagonism, perhaps toward mutualism, in cases of parasitism where host fidelity is high and availability of alternate hosts is low. In these models, host fidelity is achieved when lineages of parasites and their host are tightly linked through vertical transmission from parent to offspring.

Compelling evidence for the ‘virulence theory’ comes from interactions involving microbial parasites. For example, *Wolbachia* are endosymbiotic bacteria that live inside the cells of their invertebrate hosts. They are transmitted directly from mother to offspring, and spread through populations by manipulating the reproduction of their hosts. The most common reproductive manipulation responsible for the spread of these bacteria, called “cytoplasmic incompatibility,” arises when infected males mate with uninfected females, resulting in fewer offspring than normal. There are fitness costs for the hosts associated with *Wolbachia* infections, most commonly involving a reduction in egg production. The virulence theory predicts and evidence suggests that there is selection for the bacteria to evolve a more benign lifestyle, changing the bacterium from being parasitic to more mutualistic, where *Wolbachia*-infected hosts have higher rates of egg production than their uninfected counterparts.

Reciprocal evolutionary responses are most likely important to the evolution of symbiotic mutualisms, and subsequent diversification may be the result of the mutualism improving niche width, population size, or transition into adaptive zones.

However, with the exception of plant-pollinator interactions, it is unclear how important mutualistic coevolution is as a driving force of diversification, especially as compared to the well-established mechanisms associated with competitive and antagonistic coevolution.

Plant-pollinator interactions are powerful tools of evolution because pollinators transport gametes (via pollen) between flowers. Plant-pollinator relationships are thought to be critical to the historical diversification of angiosperm flowers. In fact, up to 25% of plant speciation events could be a result of interactions with pollinators.

The obligate pollinating seed-predation mutualisms of the yucca and yucca moth and fig and fig wasps are attributed to coevolution diversification because the intimacy of the association may prevent species from making phylogenetically drastic switches to new partners. Interacting with a distant relative of your partner may not be an option if coevolution has created incompatibilities in specialized traits required for the interaction (Figure 17.2.4).

For instance, if laying eggs into yucca flowers requires a particular complement of ovipositor traits and moth behaviors, we might predict finding host switches only between closely related yuccas. Initial analyses of yucca and yucca moth phylogenies suggest that the trees are somewhat congruent, although there have been at least two instances of moths switching hosts to quite distantly related yuccas. The interaction between yuccas and yucca moths is clearly one that is highly specialized and coevolved yet we do not find a phylogenetic pattern of perfect matching between plant and insect.

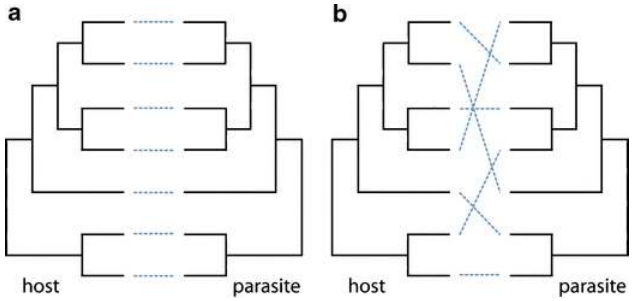


Figure 17.2.4: Comparison of host and parasite phylogenetic trees. The *dotted lines* indicate host associations of the parasites. a) Matching speciation events between host and parasite show a strict pattern of cospeciation. b) Host switches to distant relatives are shown by the crossing lines. Some parasites use closely related hosts, but most have jumped to a distant relative. Figure from Segraves 2010.

However, there is also evidence opposing the primacy of mutualistic coevolution in these relationships. Figs have been shown to be successfully pollinated regardless of pollinator species and pollinator host-switch may be more frequent than co-speciation events (Figure 17.2.5). There is also evidence that geographic isolation plays a significant role in yucca diversification. These together suggest that while coevolution plays a role in the emergence of these mutualisms, it is not the exclusive mechanism and may not even be the primary one.

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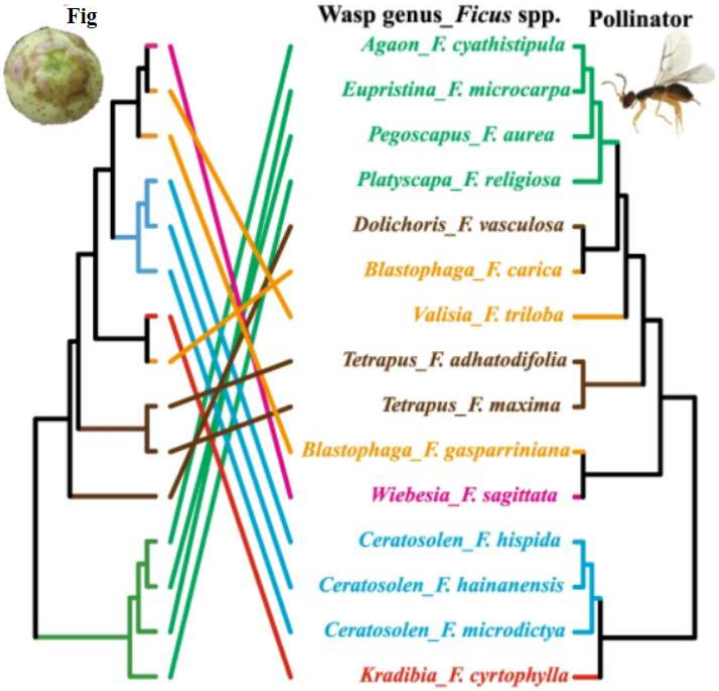


Figure 17.2.5: Cophylogenetic comparison of the pollinators associated with the 15 fig species studied. *Ficus* and pollinator phylogenies used were indicated with symbol of figs and wasp separately. Tip-name colors indicate subgeneric classification. Extensive phylogenetic incongruence is shown for each pair of phylogenies. Figure modified from Wang et al. 2021.

Attributions

This chapter was written by Aaron Howard.

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17.4: Maintenance of Mutualisms

Maintenance of mutualism

The stability of mutualisms can be undermined by cheating. Cheating is a behavior whereby organisms receive a benefit at the cost of other organisms. Cheating is common in many mutualistic and altruistic relationships (Ferriere et al. 2002). A cheater is an individual who does not cooperate (or cooperates less than their fair share) but can potentially gain the benefit from others cooperating (West et al. 2006). Cheaters are also those who selfishly use common resources to maximize their individual fitness at the expense of a group (McLean and Gudelj 2006). Simple two-player game theory and the associated evolutionary theory indicate that cheating can be evolutionarily stable, but there are mechanisms to regulate it (Foster and Kokko 2006).

The mutualism between legume plants and rhizobia (nitrogen-fixing soil bacteria) is an example where this regulation occurs. Rhizobia establish symbiotic organs termed root nodules on the roots of their host, and proliferate by extracting nutrients from the host plant. In turn, they supply their host plants with nitrogen resources produced by nitrogen gas fixation. This mutual nutrient exchange should promote the fitness of both organisms and thereby strengthen the symbiotic relationship. This beneficial effect, known as “partner fidelity feedback”, is assumed as a stabilizing factor for the mutualistic relationship (Sachs et al. 2004, Weyl et al. 2010, Friesen and Jones 2012, Friesen 2012).

On the other hand, naturally occurring rhizobium strains vary in their nitrogen fixation activity, and ineffective rhizobia that colonize their host plants without undertaking nitrogen fixation in their root nodules are ubiquitous (Gibson et al. 1975, Bottomly and Jenkins 1983, Moawad 1998, Burdon et al. 1999). Because the nitrogen fixation reaction consumes much energy (or costs), such parasitic cheaters could use surplus energy for their own growth or for synthesizing storage substances. Consequently, they are likely to proliferate more efficiently than nitrogen-fixing cooperators, posing a risk to the symbiotic interaction. Rhizobia are therefore exposed to two opposite effects that simultaneously promote (by providing benefit) and destabilize (by incurring cost) the mutualistic relationship.

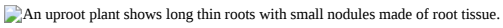


Figure 17.4.1**:** Nitrogen-fixing nodules in legumes. Photograph by Wikimedia Commons user Terraprima.

Despite the widespread presence of ineffective rhizobia, the legume–rhizobia symbiosis is evolutionarily stable. Host sanctioning is a potential mechanism that stabilizes the symbiotic interaction, where plants punish more parasitic cheaters by reducing nutrient supply based on their symbiotic performance (Friesen and Jones 2012, Friesen 2012, Kiers and Denison 1998).

Another example is found within the yucca-yucca moth mutualisms. "Cheating" sometimes happens when the yucca moth deposits too many eggs in one plant. In this case, the yucca plant has little to no benefits from this interaction. However, the plant has a unique way of sanctioning this behavior. While the sanctions against cheating often occurs directly to the individual, in this case, the constraint occurs to the individual's offspring. The yucca plant can "abort" the moths by aborting the flowers. Pellmyr and Huth (1994) found that there is selective maturation for flowers that have low egg loads and high number of scars (and therefore a high amount of pollen). In this way, there is selection against the "cheaters" who try to use the yucca plant without providing the benefits of pollination.

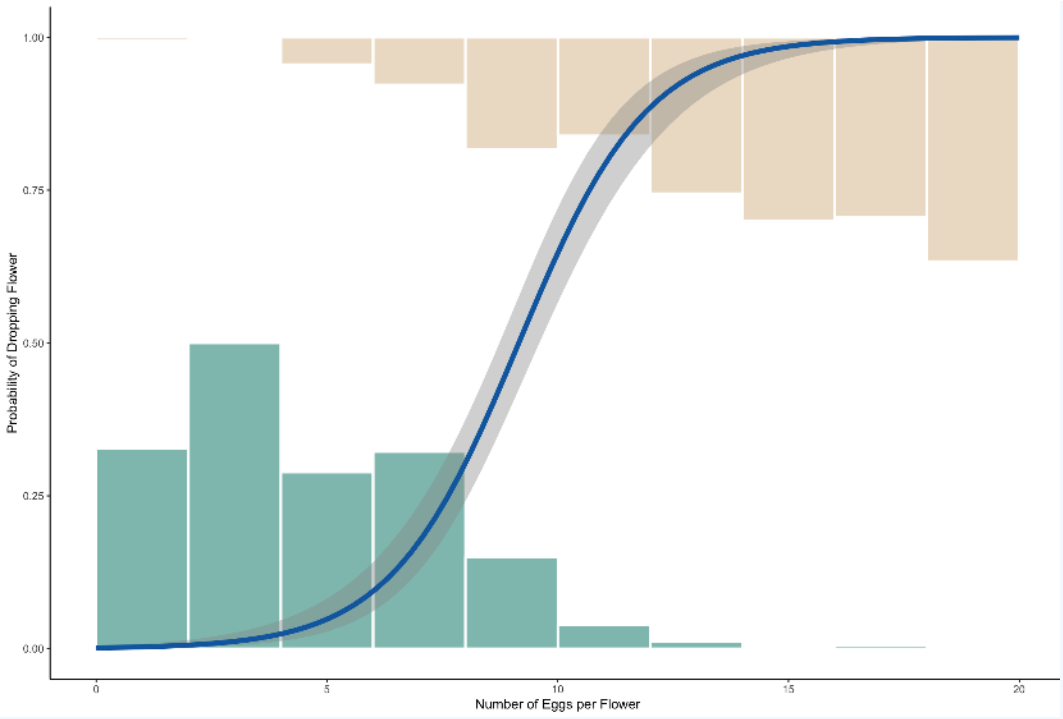


Figure 17.4.2**:** Two yucca moth females in a yucca flower. The female on the right is laying an egg and clearly shows the pollen ball on the underside of her head. The female on the left is actively pollinating with her maxillary tentacles. Photograph by Olle Pellmyr.

Exercise 17.4.1: When should you sanction a cheater?

Yucca plants will drop flowers if their obligate pollinators, the yucca moths, lay too many eggs. This reduces fitness for both the plant and the moth that laid the egg, and is a form of sanctioning by the plant. However, devoting resources to growing a fruit with too many yucca moth larvae on it would reduce the plant's fitness even more than aborting the flower does. If the flower is aborted, the cost to fitness for the pollinator is very high, making this an effective sanction against moths that try to "cheat" the plant by laying too many eggs.

Neither option is great for the plant - but at what point is it worse for the plant's fitness to retain and invest resources in a flower with too many eggs, rather than dropping the flower and sacrificing any possible surviving seeds? It turns out that most yucca fruits that are retained by the plant contain about 130 seeds, but about 20% of those seeds (26 seeds) are eaten by larvae (Alexander et al). Therefore, plants begin to drop flowers when the number of larvae present are likely to consume more than 20% of the seeds! In the graph below, you can see the probability of retaining versus dropping a flower based on the number of larvae present. This graph was simulated from the real values found by Pellmyr and Huth in their groundbreaking 1994 paper, which showed that mutualisms are not always strictly collaborative, but can involve tension between opposing forces (the plant needs pollination, but doesn't 'want' seeds eaten, the moth needs to lay as many eggs as it can) held in check by natural selection.



This graph shows the probability of retaining a flower (0) versus aborting a flower (1) based on the number of eggs laid on that flower. As the number of eggs increases, the plant becomes more likely to abort the flower, beginning to switch when there are ~6.5 larvae, meaning that most larvae eat ~4 seeds. However, as you can see from the green (retained) and tan (dropped) histograms, not every plant responds in the same way. Some plants retain flowers even with over 15 eggs laid, while others will drop flowers with only 2 eggs.

1. How many larvae could a flower tolerate if each flower had 250 seeds, instead of 130?

2. How many larvae could a flower tolerate if each larva had to eat 10 seeds, instead of 4?

Answer

1. 12.5 larvae
2. 2.6 larvae

Attributions

This chapter was written by Aaron Howard with text taken from the following CC-BY resources. Exercise text, data simulation, and code written by Castilleja Olmsted:

- **Cheating (biology) by Wikipedia, the free encyclopedia**
- Fujita H, Aoki S, Kawaguchi M (2014) Evolutionary Dynamics of Nitrogen Fixation in the Legume–Rhizobia Symbiosis. PLoS ONE 9(4): e93670. doi:10.1371/journal.pone.0093670

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Jump up to:[a] [b] [c] [d] *Foster, K. R.; Kokko, H. (2006). "Cheating can stabilize cooperation in mutualisms". Proceedings of the Royal Society B: Biological Sciences. **273** (1598): 2233–2239. doi:10.1098/rspb.2006.3571. PMC 1635526. PMID 16901844.*

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17.5: Commensalisms

Phoresis

Phoresis or **phoresy** is a non-permanent, commensalistic interaction in which one organism (a phoront or phoretic) attaches itself to another (the host) solely for the purpose of travel (White et al., 2017). Phoresis has been observed directly in ticks and mites since the 18th century (Houck & O'Connor, 1991), and indirectly in fossils 320 million years old (White et al., 2017). It is not restricted to arthropods or animals; plants with seeds that disperse by attaching themselves to animals are also considered to be phoretic (Houck, 2009).



Figure 17.5.1**:** Male *Bombus hypnorum* with phoretic mites. Photograph by Dimităr Boevski.

The strict definition of phoresis excludes cases in which the relationship is permanent (e.g. that of a barnacle surviving on a whale) or those in which the phoront gains any kind of advantage from the host organism (e.g. remoras attaching to sharks for transportation and food) (Houck & O'Connor, 1991). Phoresis is a commensal relationship and deviations result in mutualistic or parasitic relationships. Phoretic relationships can become parasitic if a cost is inflicted upon the host, such as if the number of mites on a host begins impeding its movement. Parasitic relationships could also evolve for from phoretic ones if the phoront gains a fitness advantage from the death of a host (e.g. nutrition). Mutualistic relationships could also evolve if the phoront began to confer a benefit to the host (e.g. predator defense) (White et al., 2017). The evolutionary plasticity of phoretic relationships allow them to potentially add to the complexity and diversity of ecosystems (Houck, 2009).

Cases in which the phoront parasitizes or preys upon the host organism after travel are still considered phoresis, as long as the travel behavior and the feeding or parasitizing behavior are separate (White et al., 2017). Similarly, some pseudoscorpions prey

upon the same species that act as their phoretic host. The behaviors are completely separate, however, since the pseudoscorpion uses anatomical features specifically for predation when treating the host as prey, but employs anatomical features used for phoresis when travelling (Poinar et al., 1998).

Inquilinism

An **inquiline** is an animal that lives commensally in the nest, burrow, or dwelling place of an animal of another species. For example, some organisms such as insects may live in the homes of gophers or the garages of human beings and feed on debris, fungi, and roots. The most widely distributed types of inquiline are those found in association with the nests of social insects, especially ants and termites – a single colony may support dozens of different inquiline species. The distinctions between parasites, social parasites, and inquilines are subtle, and many species may fulfill the criteria for more than one of these, as inquilines do exhibit many of the same characteristics as parasites. However, parasites are specifically *not* inquilines, because by definition they have a deleterious effect on the host species (Nash & Boomsma, 2008), while inquilines have not been confirmed to do so.

In the specific case of termites, the term "*inquiline*" is restricted to termite species that inhabit other termite species' nests (Florencio et al., 2013; Cunha et al., 2003; Hugo et al., 2019), whereas other arthropods cohabiting termitaria are called "*termitophiles*" (Rosa et al., 2018; Oliveira, 2018). It is important to reiterate that inquilinism in termites (*Blattodea*, formerly *Isoptera*) contrasts with the inquilinism observed in other eusocial insects such as ants and bees (*Hymenoptera*), even though the term "*inquiline*" has been adopted in both cases. A major distinction is that, while in the former the species mostly resemble forms of commensalism, the latter includes species currently confirmed as social parasites, thus, being closely related to parasitism.

Inquilines are known especially among the gall wasps (*Cynipidae* family). In the sub-family *Synerginae*, this mode of life predominates. These insects are similar in structure to the true gall-inducing wasp but do not produce galls, instead, they deposit their eggs within those of other species. They infest certain species of galls, such as those of the blackberry and some oak galls, in large numbers, and sometimes more than one kind occur in a single gall. Perhaps the most remarkable feature of these inquilines is their frequent close resemblance to the insect that produces the gall they infest (Rines, 2020; Discover Life, 2011).

The term *inquiline* has also been applied to aquatic invertebrates that spend all or part of their life cycles in phytotelmata, water-filled structures produced by plants (Cronk & Fennessy, 2001). For example, *Wyeomyia smithii*, *Metriocnemus knabi*, and *Habrotrocha rosa* are three invertebrates that make up part of the microecosystem within the pitchers of *Sarracenia purpurea* (Cochran-Stafira & von Ende, 1998). Some species of pitcher plants like the *Nepenthes* and *Cephalotus* produce acidic, toxic or digestive fluids and host a limited diversity of inquilines. Other pitcher plant species like the *Sarracenia* or *Heliamphora* host diverse organisms and depend to a large extent on their symbionts for prey utilization (Adkassnig et al., 2011).

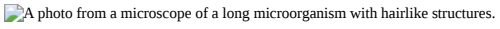


Figure 17.5.2**:** *Wyeomyia smithii* larva is an inquiline species in the pitcher leaves of *Sarracenia purpurea*. "*Wyeomyia smithii*" by Rkitko is licensed under CC BY-SA 3.0.

Metabiosis

Metabiosis is a more indirect dependency, in which one organism creates or prepares a suitable environment for a second. Examples include maggots, which develop on and infest corpses, and hermit crabs, which use gastropod shells to protect their bodies.

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CHAPTER OVERVIEW

Chapter 18: Ecological Succession

Learning Objectives

- Objective 1: Introduce succession by exploring the history of its theory
- Objective 2: Describe role of disturbance and expected outcomes regarding diversity
- Objective 3: Summarize important models of successional change
- Objective 4: Go beyond plants by investigating the roles of consumers in succession

18.1: Introduction

18.2: Effects of Disturbance

18.3: Patterns of Diversity Following Disturbance

18.4: Successional Change

18.5: The Role of Consumers and Alternate Stable States

Summary

Succession, or the process of change in the species structure of a community over time, was one of the first theories developed in ecology. Succession is brought about by environmental disturbances, and generally speaking, disturbance increases biodiversity. However, the level of disturbance significantly influences species diversity and may be maximized at intermediate levels. The patterns of successional change in biodiversity are scale dependent and must be quantified appropriately using alpha, beta, and gamma diversities. There are three common models used to explain the dynamics of community development through succession. In these models pioneer species facilitate, inhibit, or can be tolerated by later successional organisms. Succession is commonly framed within plant communities. However, animal communities affect succession through phenomena like the redirection of successional trajectories and the development of alternative stable states.

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18.1: Introduction

Ecological succession is the process of change in the species composition of an ecological community over time. It is a process by which an ecological community undergoes more or less orderly and predictable changes following a disturbance or the initial colonization of a new habitat. Succession may be initiated either by formation of new, unoccupied habitat, such as from a lava flow or a severe landslide, or by some form of disturbance of a community, such as from a fire, severe windthrow, or logging. Succession that begins in new habitats, uninfluenced by pre-existing communities is called primary succession, whereas succession that follows disruption of a pre-existing community is called secondary succession.

18.1.1: History of succession

Succession was among the first theories advanced in the ecological literature. Ecological succession was first documented in the Indiana Dunes of Northwest Indiana and remains an important ecological topic of study (Smith & Mark, 2009).

Between 1899-1910, Henry Chandler Cowles, at the University of Chicago, developed a more formal concept of succession. Inspired by studies of Danish dunes by Eugen Warming, Cowles studied vegetation development on sand dunes on the shores of Lake Michigan (the Indiana Dunes). He recognized that vegetation on dunes of different ages might be interpreted as different stages of a general trend of vegetation development on dunes (an approach to the study of vegetation change later termed space-for-time substitution, or chronosequence studies).

From about 1900 to 1960, however, understanding of succession was dominated by the theories of Frederic Clements, a contemporary of Cowles, who held that **seres** were highly predictable and deterministic series of successional plant communities that converged on a climatically determined stable climax community regardless of starting conditions. Clements explicitly analogized the successional development of ecological communities with ontogenetic development of individual organisms, and his model is often referred to as the pseudo-organismic theory of community ecology. Clements and his followers developed a complex taxonomy of communities and successional pathways.

Henry Gleason offered a contrasting framework as early as the 1920s. The Gleasonian model was more complex and much less deterministic than the Clementsian. It differs most fundamentally from the Clementsian view in suggesting a much greater role of chance factors and in denying the existence of coherent, sharply bounded community types. Gleason argued that species distributions responded individualistically to environmental factors, and communities were best regarded as artifacts of the juxtaposition of species distributions. Gleason's ideas, first published in 1926, were largely ignored until the late 1950s.

Two quotes illustrate the contrasting views of Clements and Gleason. Clements wrote in 1916:

> *The developmental study of vegetation necessarily rests upon the assumption that the unit or climax formation is an organic entity. As an organism the formation arises, grows, matures, and dies. Furthermore, each climax formation is able to reproduce itself, repeating with essential fidelity the stages of its development.*
>
> *— Frederic Clements (1916)*

while Gleason, in his 1926 paper, said:

> *An association is not an organism, scarcely even a vegetational unit, but merely a coincidence.*
>
> *— Henry Gleason (1926)*

Gleason's ideas were, in fact, more consistent with Cowles' original thinking about succession. About Clements' distinction between primary succession and secondary succession, Cowles wrote (1911):

> *This classification seems not to be of fundamental value, since it separates such closely related phenomena as those of erosion and deposition, and it places together such unlike things as human agencies and the subsidence of land.*

> — *Henry Cowles*

Succession theory was developed primarily by botanists. The study of succession applied to whole ecosystems initiated in the writings of Ramon Margalef, while Eugene Odum's publication of *The Strategy of Ecosystem Development* is considered its formal starting point (Bazzaz, 1996).

Animal life also exhibits changes with changing communities. In the lichen stage fauna is sparse. It comprises a few mites, ants and spiders living in cracks and crevices. The fauna undergoes a qualitative increase during the herb grass stage. The animals found during this stage include nematodes, insects larvae, ants, spiders, mites, etc. The animal population increases and diversifies with the development of the forest climax community. The fauna consists of invertebrates like slugs, snails, worms, millipedes, centipedes, ants, bugs; and vertebrates such as squirrels, foxes, mice, moles, snakes, various birds, salamanders and frogs.

A more rigorous, data-driven testing of successional models and community theory generally began with the work of Robert Whittaker and John Curtis in the 1950s and 1960s. Succession theory has since become less monolithic and more complex. J. Connell and R. Slatyer attempted a codification of successional processes by mechanism. Among British and North American ecologists, the notion of a stable climax vegetation has been largely abandoned, and successional processes have come to be seen as much less deterministic, with important roles for historical contingency and for alternate pathways in the actual development of communities. Debates continue as to the general predictability of successional dynamics and the relative importance of equilibrial vs. non-equilibrial processes. Former Harvard professor Fakhri A. Bazzaz introduced the notion of *scale* into the discussion, as he considered that at local or small area scale the processes are stochastic and patchy, but taking bigger regional areas into consideration, certain tendencies can not be denied (1996).

View this video for a short summary of ecological succession before you continue to explore some of the key concepts involved in this chapter.



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18.2: Effects of Disturbance

Changes in community structure and composition over time are induced by environmental disturbances such as volcanoes, earthquakes, storms, fires, and climate change. Communities with a stable structure are said to be at equilibrium. Following a disturbance, the community may or may not return to the equilibrium state. In primary succession, newly exposed or newly formed land is colonized by living things; in secondary succession, part of an ecosystem is disturbed and remnants of the previous community remain. Thus, disturbance can initiate successional change.

Species that are well adapted for exploiting disturbance sites are referred to as pioneers or early successional species. These shade-intolerant species are able to photosynthesize at high rates, produce a lot of offspring, and grow and mature quickly. Their fast growth is usually balanced by short life spans. Furthermore, although these species often dominate immediately following a disturbance, they are unable to compete with shade-tolerant species later on and are replaced by these species through succession. However these shifts may not reflect the progressive entry to the community of the taller long-lived forms, but instead, the gradual emergence and dominance of species that may have been present, but inconspicuous directly after the disturbance (Nobel, n.d.). Disturbances have also been shown to be important facilitators of non-native plant invasions (Lembrechts, 2016).

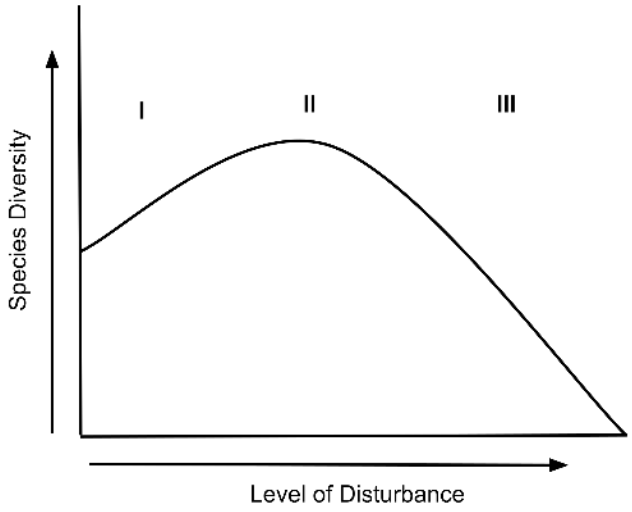
While plants must deal directly with disturbances because of their lack of mobility, many animals are mobile and thus are not as immediately affected by disturbance. For example, some animals could successfully evade the initial destruction of a forest fire, but can later return to the burned area and thrive on new growth on the forest floor. Disturbed communities (such as a forest after a fire) often support a wider variety of plants compared to pre-disturbance vegetation. The plants in turn support a variety of wildlife, temporarily increasing biological diversity in the forest (Pringle, 1979).

18.2.1: Intermediate Disturbance Hypothesis

The intermediate disturbance hypothesis (IDH) suggests that local species diversity is maximized when ecological disturbance is neither too rare nor too frequent. At low levels of disturbance, more competitive organisms will push subordinate species to extinction and dominate the ecosystem (Dial & Roughgarden, 1988). At high levels of disturbance, due to frequent forest fires or human impacts like deforestation, all species are at risk of going extinct. According to intermediate disturbance hypothesis theory, at intermediate levels of disturbance, diversity is thus maximized because species that thrive at both early and late successional stages can coexist. Intermediate disturbance hypothesisis a nonequilibrium model used to describe the relationship between disturbance and species diversity.

The intermediate disturbance hypothesis is based on the following premises:

1. ecological disturbances have major effects on species richness within the area of disturbance,
2. interspecific competition results from one species driving a competitor to extinction and becoming dominant in the ecosystem, and
3. moderate ecological scale disturbances prevent interspecific competition (Wilkinson, 1999; Kricher, 2011; Catford et al., 2012).



https://bio.libretexts.org/@go/page/92890

Figure 18.2.1**:** I describes how, at low levels of ecological disturbance species richness decreases as competitive exclusion increases; II shows that at intermediate levels of disturbance, diversity is maximized because species that thrive at both early and late successional stages can coexist; III shows that at high levels of disturbance species richness is decreased due to an increase in species movement. "Intermediate Disturbance Hypothesis Graph" by Sciencerelatedusername is licensed under CC BY-SA 4.0.

Disturbances act to disrupt stable ecosystems and clear species' habitat. As a result, disturbances lead to species movement into the newly cleared area (secondary succession) (Wilkinson, 1999). Once an area is cleared there is a progressive increase in species richness and competition between species takes place. Once the conditions that create a disturbance are gone, and competition between species in the formerly disturbed area increases, species richness decreases as competitive exclusion increases (Vandermeer et al., 1996).

"Gause's Law", also known as competitive exclusion, explains how species that compete for the same resources cannot coexist in the same niche (Kricher, 2011). Each species handles change from a disturbance differently; therefore, intermediate disturbance hypothesis can be described as both "broad in description and rich in detail" (Wilkinson, 1999). The broad intermediate disturbance hypothesis model can be broken down into smaller divisions which include spatial within-patch scales, spatial between-patch scales, and purely temporal models. Each subdivision within this theory generates similar explanations for the coexistence of species with habitat disturbance. Joseph H. Connell proposed that relatively low disturbance leads to decreased diversity and high disturbance causes an increase in species movement (1978). These proposed relationships lead to the hypothesis that intermediate disturbance levels would be the optimal amount of disorder within an ecosystem.

Another way of thinking about the intermediate disturbance hypothesis requires that we consider the types of organisms that could specialize in areas with different levels of disturbance. K-selected species generally demonstrate more competitive traits. Their primary investment of resources is directed towards growth, causing them to dominate stable ecosystems over a long period of time. In contrast, r-selected species colonize open areas quickly and can dominate landscapes that have been recently cleared by disturbance (Catford et al., 2012). These characteristics attribute to the species that thrive in habitats with higher and lower amounts of disturbance. Based on the contradictory characteristics of both of these examples, areas of occasional disturbance allow both r and K species to flourish in the same area. If K-selected and r-selected species can live in the same region, species richness can reach its maximum.

Several alternative hypotheses to the intermediate disturbance hypothesis have been proposed (Hall et al., 2012). One alternative hypothesis states that the species diversity in a disturbance-mediated coexistence between species is maximized by the presence of a disturbance regime resembling the historic processes. This is because species generally adapt to the level of disturbance in their ecosystem through evolution (whether disturbance is of high, intermediate or low level). In addition, many species (e.g. ruderal plants and fire-adapted species) even depend on a specific disturbance in ecosystems where it often occurs.

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18.3: Patterns of Diversity Following Disturbance

In general, communities in early succession will be dominated by fast-growing, well-dispersed species (opportunist, fugitive, or r-selected life-histories). As succession proceeds, these species will tend to be replaced by more competitive (K-selected) species (See Life History Strategies). Trends in ecosystem and community properties in succession have been suggested, but few appear to be general. For example, species diversity almost necessarily increases during early succession as new species arrive, but may decline in later succession as competition eliminates opportunistic species and leads to dominance by locally superior competitors.

Ecological succession was formerly seen as having a stable end-stage called the climax, sometimes referred to as the 'potential vegetation' of a site, and shaped primarily by the local climate. This idea has been largely abandoned by modern ecologists in favor of non-equilibrium ideas of ecosystems dynamics (See Intermediate Disturbance Hypothesis). Most natural ecosystems experience disturbance at a rate that makes a "climax" community unattainable. Climate change often occurs at a rate and frequency sufficient to prevent arrival at a climax state. Additions to available species pools through range expansions and introductions can also continually reshape communities.

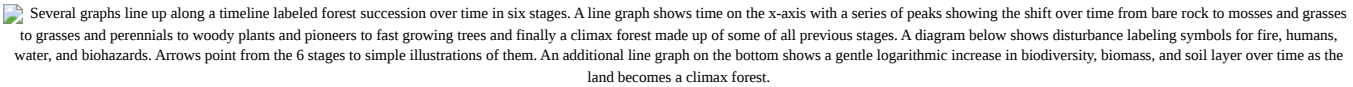


Figure 18.3.1**:** Trajectory of forest secondary succession following an intense disturbance, resulting in nearly no original biomass, to a mature forest state. Biodiversity, biomass, and soil depth all increase with time, and community composition changes. Image by Lucas Martin Frey is licensed under CC BY 3.0.

18.3.1: Patterns of Diversity in Primary vs. Secondary Succession

Primary succession begins on rock formations, such as volcanoes or mountains, or in a place with no organisms or soil (eg, an abandoned parking lot or railroad). In primary succession pioneer species like lichen, algae and fungi as well as abiotic factors like wind and water start to develop soil and initiate other important mechanisms for greater diversity to flourish. These pioneer species are then replaced by plants better adapted to less harsh conditions, these plants include vascular plants like grasses and some shrubs that are able to live in thin soils that are often mineral-based. Water and nutrient levels increase with the amount of succession exhibited (Fujiyoshi et al., 2005).

The early stages of primary succession are dominated by species with small propagules (seed and spores) which can be dispersed long distances. The early colonizers—often algae, fungi, and lichens—stabilize the substrate. Nitrogen supplies are limited in new soils, and nitrogen-fixing species tend to play an important role early in primary succession (Korablev & Neshataeva, 2016).

Successional dynamics following severe disturbance or removal of a pre-existing community are called **secondary succession**. Dynamics in secondary succession are strongly influenced by pre-disturbance conditions, including soil development, seed banks, remaining organic matter, and residual living organisms. Because of residual fertility and pre-existing organisms, community change in early stages of secondary succession can be relatively rapid. Secondary succession is much more commonly observed and studied than primary succession. Particularly common types of secondary succession include responses to natural disturbances such as fire, flood, and severe winds, and to human-caused disturbances such as logging and agriculture.

Unlike in primary succession, the species that dominate secondary succession, are usually present from the start of the process, often in the soil seed bank. In some systems the successional pathways are fairly consistent, and thus, are easy to predict. In others, there are many possible pathways, potentially leading to *alternative stable states*. For example, nitrogen-fixing legumes alter successional trajectories (Chapin et al., 2002).

18.3.2: Patterns of Diversity at Different Scales

While we will discuss ways to measure biodiversity more in a later chapter (see section 22.2 on Diversity Indices), it's helpful to have some vocabulary to describe patterns of biodiversity when talking about succession and disturbance.

How is biodiversity measured? Part 1, Alpha, Beta, and Gamma Diversity 18.3.1

Alpha diversity (**α-diversity**) is the mean species diversity in a site at a local scale. At it's simplest, it is the number of species in a given location. More complex metrics of diversity take into account not only how many species there are, but how even their abundances are. Examples of places with extremely high alpha diversity include tropical rainforests.

Beta diversity (**β-diversity**) is the ratio between regional and local species diversity and connects alpha and gamma diversity. It describes the rate at which species composition changes across a region. For example, if every wetland in a region was inhabited by a similar suite of plant species, then the region would have low beta diversity; in contrast, if several wetlands in a region had plants communities that were distinct and had little overlap with one another, the region would have high beta diversity. Beta diversity is calculated as gamma diversity divided by alpha diversity. Beta diversity as a measure of species turnover overemphasizes the role of rare species. The difference in species composition between two sites or communities likely reflects the presence and absence of some rare species in the assemblages. Examples of places with high beta-diversity include matrices of recently disturbed and undisturbed land.

Gamma diversity (**γ-diversity**) is the total species diversity in a landscape. Here, questions of scale become very important to appropriately distinguish between alpha and gamma diversity.

These terms were introduced by R. H. Whittaker (1960; 1974). Whittaker's idea was that the total species diversity in a landscape (gamma diversity) is determined by two different things, the mean species diversity in sites at a more local scale (alpha diversity) and the differentiation among those sites (beta diversity). This idea can be mathematically notated in this way: $\beta=\gamma/\alpha$. The simplest calculations of alpha and beta diversity involve reworking this equation algebraically, with the result being that alpha, beta, and gamma diversity scale together.

Disturbance and following successional change can increase biodiversity at the alpha, beta, and gamma scales, although the patterns of diversity increase are scale dependent. For instance, a recently disturbed area might have higher alpha diversity than an undisturbed area but this is a result of different patches within the area where existing biomass either was or was not removed, allowing for colonization by novel species. Thus, it is not always clear whether the increase in diversity should be attributed to alpha or gamma diversity. However, the presence of patches in different successional stages also increases beta diversity (and gamma diversity) by supporting cohorts of species with different life history traits and characteristics in the same landscape, whether or not the straightforward number of species present in any given patch is higher than any other patch. Simply comparing alpha diversity in each patch might not demonstrate the impact disturbance has on patterns of biodiversity, whereas calculating beta and gamma diversity provide a more accurate picture.

Exercise 18.3.1: Calculating Alpha, Beta, and Gamma diversity

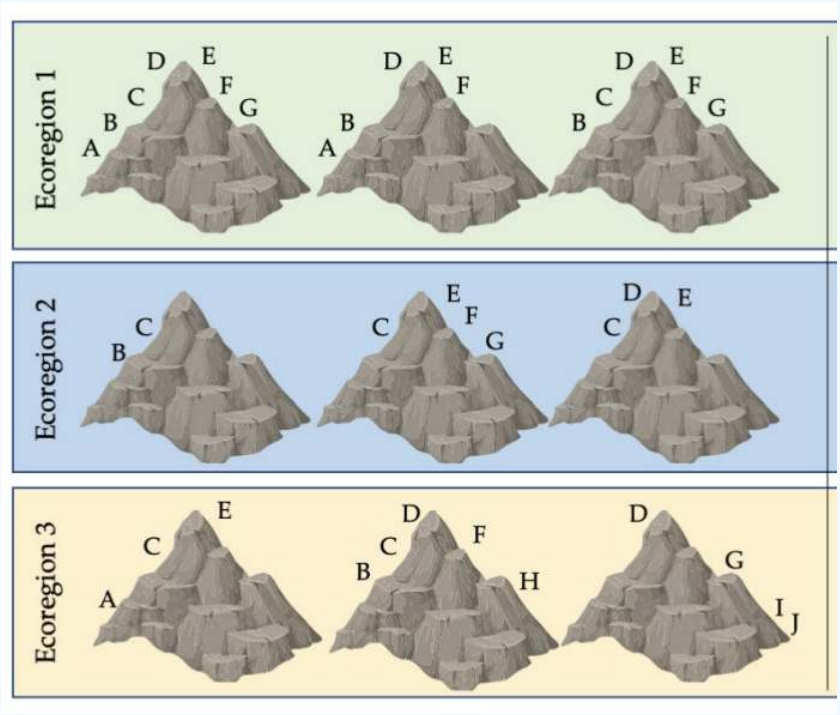
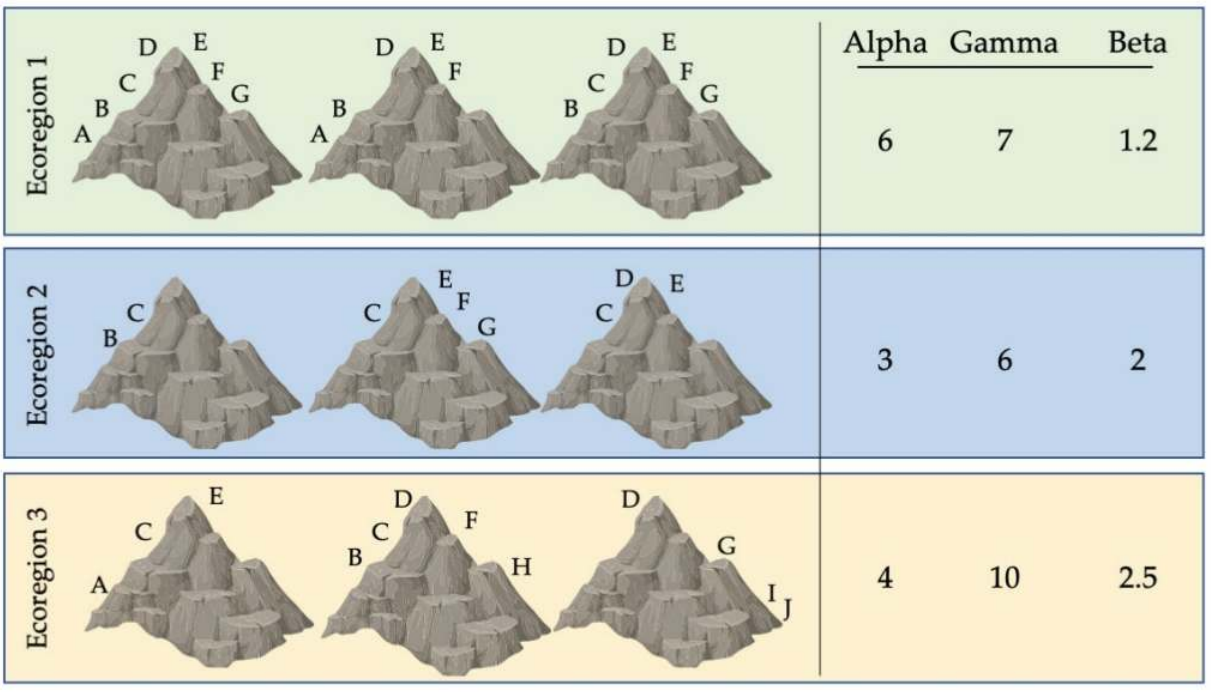


Figure 18.3.2*a*: This figure shows biodiversity for nine mountain peaks across three Ecoregions. Each symbol represents a different species; some species have populations on only one peak, while others are found on two or more peaks.

1. Calculate alpha, beta, and gamma diversity for each mountain/Ecoregion.
2. Does the "most diverse" mountain or Ecoregion change depending on which metrics we use?

Answer



	Alpha	Gamma	Beta
Ecoregion 1	6	7	1.2
Ecoregion 2	3	6	2
Ecoregion 3	4	10	2.5

Figure 18.3.2*b***:** Calculations for each alpha, beta, and gamma measurements of the three ecoregions are shown.

Ecoregion 1 has the highest highest average species richness (alpha diversity) across its three peaks. If we were only to look at average alpha diversity, we might consider it the most diverse region. However, Ecoregion 3 has much higher turnover (beta diversity) and higher species diversity at the landscape scale. Furthermore, all of the species represented in Ecoregions 1 and 2 are also represented in Ecoregion 3.

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- https://en.wikipedia.org/wiki/Beta_diversity
- https://en.wikipedia.org/wiki/Alpha_diversity
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18.4: Successional Change

The trajectory of successional change can be influenced by site conditions, by the type of events initiating succession, by the interactions of the species present, and by more stochastic factors such as availability of propagules or weather conditions at the time of disturbance. Some of these factors contribute to predictability of succession dynamics; others add more probabilistic elements.

Autogenic succession can be brought by changes in the soil caused by the organisms there. These changes include accumulation of organic matter in litter or humic layer, alteration of soil nutrients, or change in the pH of soil due to the plants growing there. The structure of the plants themselves can also alter the community. For example, when larger species like trees mature, they produce shade on to the developing forest floor that tends to exclude light-requiring species. Shade-tolerant species will invade the area.

Allogenic succession is caused by external environmental influences and not by the vegetation. For example, soil changes due to erosion, leaching or the deposition of silt and clays can alter the nutrient content and water relationships in the ecosystems. Animals also play an important role in allogenic changes as they are pollinators, seed dispersers and herbivores. They can also increase nutrient content of the soil in certain areas, or shift soil about (as termites, ants, and moles do) creating patches in the habitat. This may create regeneration sites that favor certain species.

Climatic factors may be very important, but on a much longer time-scale than any other. Changes in temperature and rainfall patterns will promote changes in communities. As the climate warmed at the end of each ice age, great successional changes took place. The tundra vegetation and bare glacial till deposits underwent succession to mixed deciduous forest. The greenhouse effect resulting in increase in temperature is likely to bring profound Allogenic changes in the next century. Geological and climatic catastrophes such as volcanic eruptions, earthquakes, avalanches, meteors, floods, fires, and high wind also bring allogenic changes.

18.4.1: Models of Successional Change

Joseph Connell and Ralph Slatyer further developed the understanding of successional mechanisms in their 1977 paper and proposed that there were 3 main modes of successional development. These sequences could be understood in the context of the specific life-history theories of the individual species within an ecological community.

Facilitation model

The facilitation model is based on the assumption that only particular species with qualities ideal for "early succession" can colonize the newly exposed landforms after an ecological disturbance.

- These "colonizing" qualities include: highly effective methods of dispersal, the ability to remain dormant for long periods of time, and a rapid growth rate. However, the pioneer species are often subsequently less successful once an area has been heavily populated by surrounding species due to increased shade, litter or concentrated roots in the soil, etc. (Connell & Slatyer, 1977).
- Thus, the presence of early successional species often changes the environment so that the habitat is less hospitable for the original species' own ecological demands and facilitates the invasion of later-successional species.

The facilitation model suggests that the presence of an initial species aids and increases the probability of the growth of a second species. For example, the presence of alder plants aids the growth of willow and poplar seedlings in an Alaskan floodplain (Walker & Chapin, 1986). Alder roots contain nitrogen-fixing bacteria, which greatly increase the amount of inorganic nitrogen present in soils. This increased availability of nitrogen aids the growth of both willow and poplar seedlings in areas without other competition. Eventually, however, willow and poplar grow more rapidly than alder, leading to a reduction in the abundance of the pioneer species, and eventually, spruce becomes a later-succession species, due to its increased ability (over alder) to grow in shaded areas.

Another case of facilitation comes from the colonization of lakeshore sand dunes (Connell & Slatyer, 1977; Walker et al., 1986). Adjacent pioneer plants colonize the otherwise moving sands and alter the environmental constraints of the sandy environment to better suit other plant species, which can then allow for soil binding to take place (National Biological Information Infrastructure, 2011). The giant saguaro cactus, in this respect, can only survive in the shade of other plants (or in some cases rocks) – pioneer species facilitate their existence by providing shade. (The argument has also been made that this type of interaction is exemplary of the tolerance model; see below) (Connell & Slatyer, 1977).

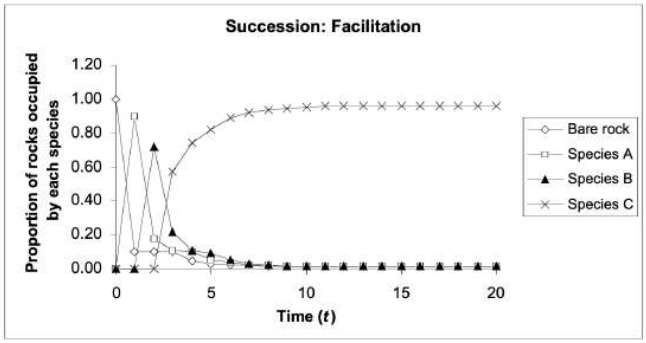


Figure 18.4.1**:**
Bare rock is frequently replaced by species A, species A by species B, and species B by species C. All these species are equally likely to be replaced by bare rock. Species C is unique in that it is almost always replaced by itself, only rarely by bare rock, and never by other species.

Source: Donovan and Welden.

Tolerance model

In this case, new pioneer species neither inhibit nor facilitate the growth and success of other species. The sequences of succession are thus entirely dependent on life-history characteristics such as the specific amount of energy a species allocates to growth (Connell & Slatyer, 1977).

- The climax community is composed of the most "tolerant" species that can co-exist with other species in a more densely populated area. Eventually, dominant species replace or reduce pioneer species abundance through competition.

The tolerance model is completely dependent upon life history characteristics. Each species has an equally likely chance to establish itself in the early stages of succession and their establishment results in no environmental changes or impacts on other species (Moorcroft, 2011). Eventually, early species, typically dominated by r-selected species, which prioritize fast rates of reproduction, are out-competed by K-selected species (species that become more dominant when there is competition for limited resources).

For example, we can examine succession in the Loess Plateau in China, where there is initial dominance of the *Artemisia scoparia* (virgate wormwood), the pioneer species. Over time, however, the *Bothriochloa ischaemum* (yellow bluestem) becomes the dominant species and the abundance of *A. scoparia* greatly declines. This is due to the rapid rate of reproduction of the *A. scoparia*, resulting in the species' early abundance, and the dominant competition from the K-selected *B. ischaemum*, resulting in that species' later abundance (Wang, 2002).

A characteristic that is often associated with the tolerance model and well documented in forest succession is survival in conditions of shade. As an uninhabited area becomes populated by different plant species, shade increases – which makes less light available for the next generation. Species that are better adapted to shady conditions will then become dominant.

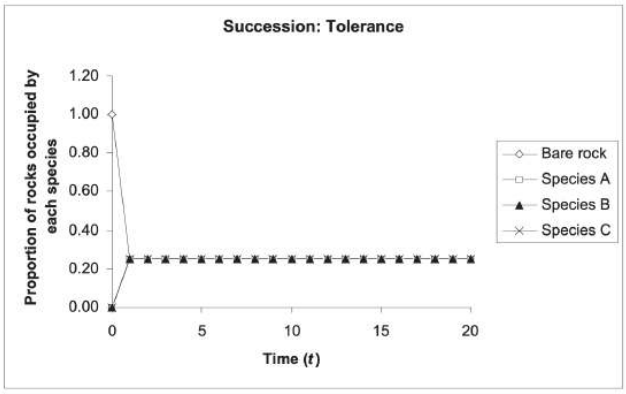


Figure 18.4.2**:** Any species is equally likely to replace any other, and equally susceptible to disturbance. *Source: Donovan and Welden*.

Inhibition model

Earlier successional species actually inhibit growth of later successional species and reduce growth of colonizing species already present (Connell & Slatyer, 1977).

- Example: Pioneer species might modify the environment through rapid growth and make the area increasingly shady (essentially increasing competition for light).
- The environment is thus less hospitable to other potential colonizing species.
- The only possibility for new growth/colonization in this successional sequence arises when a disturbance leads to dominating species being destroyed, damaged, or removed. This frees up resources and allows for the invasion of other species that were not previously present.

In this model, one species inhibits the presence of another, either through direct means, such as predation (by eating the other species or attacking them), or indirect means, such as competition for resources.

Sometimes in inhibition models, the time of establishment of a species determines which species becomes dominant. This phenomenon is referred to as the priority effect and suggests that the species that became established earlier are more likely to become the dominant species. One example of the inhibition model, and the priority effect, occurs in South Australia. In areas where bryozoans are established first, tunicates and sponges cannot grow.

The inhibition model has also been observed at work in forest ecosystems; in these systems the early arrivers hold a monopoly on the land, keeping other species out. Closed shrub canopies have been known to prevent tree growth and access to land for periods of up to 45 years – in an experimental study on inhibition it was found that areas occupied by large areas of Lantana (*Lantana camara)* sprawling shrubs excluded and inhibited the growth of tree species (Connell & Slatyer, 1977; Ricklefs, 2008).

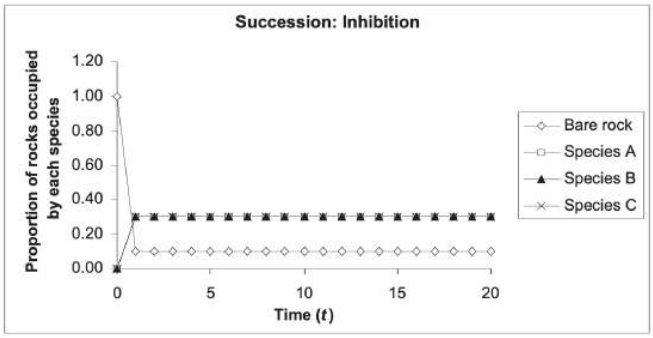


Figure 18.4.3**:** Each species is equally likely to colonize bare rock, and all species are equally susceptible to disturbance. Each species holds its site and inhibits occupancy by all others, so replacement occurs only by disturbance. *Source: Donovan and Welden*.

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- https://en.wikipedia.org/wiki/Ecological_succession
- https://en.wikipedia.org/wiki/Connell%E2%80%93Slatyer_model_of_ecological_succession
- Donovan and Welden https://blog.uvm.edu/tdonovan-vtcfwru/files/2020/06/28-Donovan-pages-115-EE.pdf

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18.5: The Role of Consumers and Alternate Stable States

18.5.1: Succession in Consumers

Animal communities also undergo change throughout successional time. In the lichen stage fauna is sparse. It comprises a few mites, ants and spiders living in cracks and crevices. The fauna undergoes a qualitative increase during the herb grass stage. The animals found during this stage include nematodes, insects larvae, ants, spiders, mites, etc. The animal population increases and diversifies with the development of the forest climax community. The fauna consists of invertebrates like slugs, snails, worms, millipedes, centipedes, ants, bugs; and vertebrates such as squirrels, foxes, mice, moles, snakes, various birds, salamanders and frogs. The pioneering fauna will colonize an area only after flora and fungi have inhabited the area. Soil fauna, ranging from microscopic protists to larger invertebrates, have a role in soil formation and nutrient cycling. Bacteria and fungi are the most important groups in the breakdown of organic detritus left by primary producing plants such as skeletal soil, moss and algae. Soil invertebrates enhance fungal activity by breaking down detritus. As soil develops, earthworms and ants alter soil characteristics. Worm burrows aerate soil and ant hills alter sediment particle size dispersal, altering soil character profoundly.

Though vertebrates in general would not be considered pioneer species, there are exceptions. Natterjack toads are specialists in open, sparsely vegetated habitats which may be at an early seral stage (Faucher et al., 2017). Wide-ranging generalists visit early succession stage habitats, but are not obligate species of those habitats because they use a mosaic of different habitats. Vertebrates can effect early seral stages. Herbivores may alter plant growth. Fossorial mammals could alter soil and plant community development. In a profound example, a seabird colony transfers considerable nitrogen into infertile soils, thereby altering plant growth. A keystone species may facilitate the introduction of pioneer species by creating new niches. For example, beavers may flood an area, allowing new species to immigrate (Wallwork, 1970).

Succession of micro-organisms including fungi and bacteria occurring within a microhabitat is known as microsuccession or serule. Like in plants, microbial succession can occur in newly available habitats (primary succession) such as surfaces of plant leaves, recently exposed rock surfaces (i.e., glacial till) or animal infant guts, and also on disturbed communities (secondary succession) like those growing in recently dead trees, decaying fruits, or animal droppings (Ortiz-Álvarez et al., 2018; Martin et al., 2021).

18.5.2: Alternative Stable States

One of the main ways consumers can affect succession is through the redirection of successional trajectories. By preferentially consuming some species, consumers can change the direction of succession, resulting in a different community type than would typically be predicted. Expected successional trajectories are predicted based on the observation of community changes through time, or through space-for-time substitutions where stands of different ages are compared, with the expectation that the youngest stands will grow to look like the oldest as time passes. However, given substantial perturbations, communities may end up going down an entirely different path than we would predict. Sometimes, they will even get "stuck" in this state, and never return to look as we would expect. This becomes especially problematic when they place they get "stuck" is low-diversity or dominated by invasive species, and makes it very hard to restore healthy ecosystems.

We can visualize a community about to undergo succession as a ball about to roll down a hill. The trajectory of succession is predictable, and gravity will pull the ball to the bottom of the hill. Disturbance can provide energy to push the ball back up the hill, but it should consistently return to the same stable end point. However, the ball may exist in a landscape with many low points, where the ball would have to roll far up a hill to change positions. Thus, there may be several **alternative stable states** where the community will be resistant to change. Catalysts, such as invasive species or ecosystem engineering animals can push the ball over a peak and into a different valley, resulting in a different endpoint to our successional trajectory. At this point, even a disturbance may not provide enough energy to push the ball all the way back up the hill and over a peak into the original successional trajectory. The new endpoint is stable, and hard to restore from.

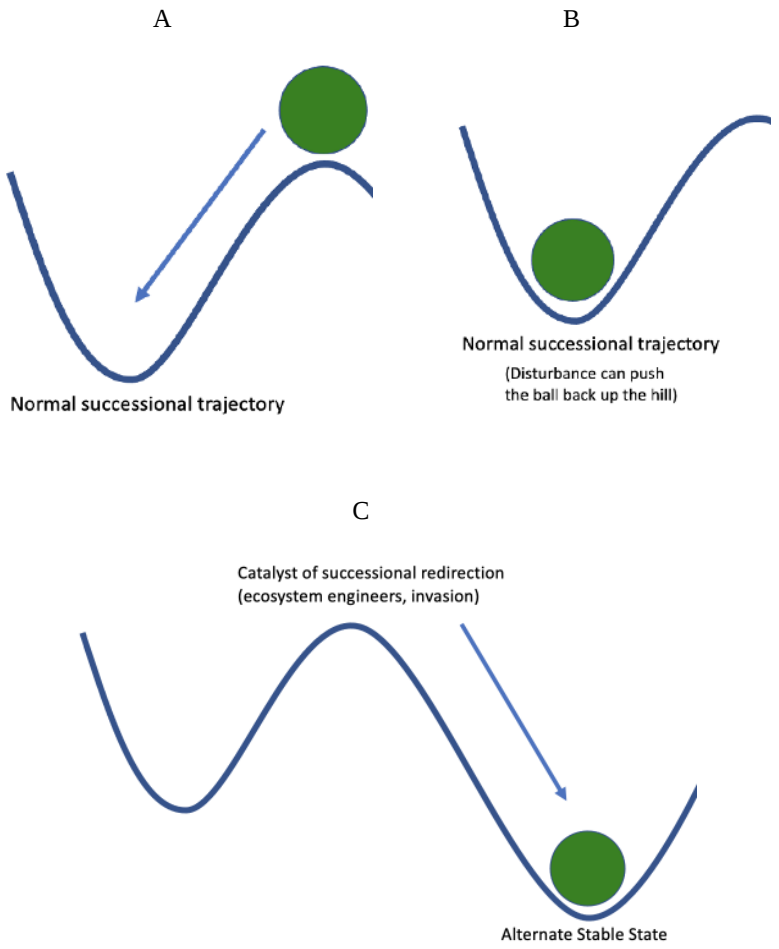


Figure 18.5.1**:** a) the starting point of early succession, which should proceed "downhill" along a predictable trajectory. b) the stable climax community at the end of a successional trajectory. c) some catalyst has pushed our community out of its original state and into an alternative stable community state.

Box18.5.1: Moose range expansions and implications for succession

As the cover of forested land increases and the climate warms, moose (*Alces alces americana*) are expanding their range on the northern and southern edges, even as far south as Connecticut (Wildlife of Connecticut , n.d.). Moose often spend time in early-successional forests because of the high-availability of young tree and shrub growth to browse on. Moose not only browse the tips of trees, reducing their ability to grow vertically, but they can actually break trees in half as they try to reach the palatable tips of branches and leaves. As a result, moose may be redirecting the trajectory of early-successional forests, especially in the southernmost edges of their range, in Connecticut, by preferentially browsing certain species of trees while avoiding others (Olmsted, 2021).

A typical successional trajectory for a mixed-hardwood forest in Connecticut would look something like this:



Figure 18.5.2*A*: Typical successional trajectory.

However, when moose browsing is added to the equation, we would expect one of two possible outcomes.

1. If moose browse all species equally and they are sufficiently abundant, they may actually delay succession, keeping the forest in a more-open, shorter state (the ball takes longer to roll down the hill).



Figure 18.5.2*B*: Possible outcome of typical successional trajectory when moose are added to the scenario, where the moose delay the succession development rate.

2. If moose browse preferentially, avoiding species they dislike (such as Spruce), they may redirect the trajectory of the forest. The mature forest which eventually takes hold will be dominated by these browse-resistant tree species, and the community composition will look very different than the trajectory in the absence of moose.



Figure 18.5.2*C*: Alternate possible outcome of typical successional trajectory when moose are added to the scenario, where the moose redirect the species diversity.

Both of these outcomes occur where moose are present, but which outcome we see is contingent on the abundances of preferred and non-preferred tree species. In the first case, if moose are controlled or removed in the third time point, the closed forest should eventually look like the original successional trajectory. However, in the second case, even if moose are no longer present in the third time point (this is likely, because moose frequent open, younger forests), the forest will still be dominated by browse-tolerant unpalatable tree species. It will no longer resemble the expected successional trajectory, and it will be unlikely to revert without major disturbance. The ability of moose to redirect succession in this way makes them an example of an ecosystem engineer. In the second case, by keeping forests open and in an early successional stage for longer, moose provide habitat and maintain food resources for many species of bird and other small animals.

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CHAPTER OVERVIEW

Chapter 19: Food Webs

Learning Objectives

- Differentiate among the components of food webs, the sources of energy to food webs, and the types of food webs
- Use quantifiable characteristics to describe and compare food webs
- Appreciate the key ecosystem role that apex predators play through trophic cascades

19.1: Introduction to and Components of Food Webs
19.2: Quantifying Food Webs
19.3: Trophic Cascades
19.4: References and Attributions

Summary

The food webs of all ecosystems have autotrophs at the base; these producers may fix carbon using energy from the sun (photoautotrophs) or from specific chemical compounds (chemoautotrophs). The energy produced at the base of the food web moves through several levels of heterotrophs, including detritivores, herbivores, omnivores, and carnivores, but some of this energy is lost during each transfer up the food web. When the apex predator or keystone predator of an ecosystem is removed, this can result in a trophic cascade that impacts the entire food web. Food webs are extremely complex, and cannot be easily depicted on paper, so the food webs we see are simplifications of reality; the simplest form is a food chain, which involved a linear sequence of interactions from primary producer to apex predator. Scientists quantify food webs by calculating transfer efficiency, food web length, and food web connectance.

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19.1: Introduction to and Components of Food Webs

Introduction

All living things require energy in one form or another. Energy is required by most complex metabolic pathways (often in the form of adenosine triphosphate, ATP), especially those responsible for building large molecules from smaller compounds, and life itself is an energy-driven process. Living organisms would not be able to assemble macromolecules (proteins, lipids, nucleic acids, and complex carbohydrates) from their monomeric subunits without a constant energy input.

Food webs illustrate how energy flows directionally through ecosystems, including how efficiently organisms acquire it, use it, and how much remains for use by other organisms of the food web.

Food Chains and Food Webs

In ecology, a **food chain** is a linear sequence of organisms through which nutrients and energy pass: primary producers, primary consumers, and higher-level consumers are used to describe ecosystem structure and dynamics. There is a single path through the chain.

Food chains do not accurately describe most ecosystems. Even when all organisms are grouped into appropriate trophic levels, some of these organisms can feed on species from more than one trophic level; likewise, some of these organisms can be eaten by species from multiple trophic levels. In other words, the linear model of ecosystems, the food chain, is not completely descriptive of ecosystem structure. A holistic model—which accounts for all the interactions between different species and their complex interconnected relationships with each other and with the environment—is a more accurate and descriptive model for ecosystems. A food web is a graphic representation of a holistic, nonlinear web of primary producers, primary consumers, and higher-level consumers used to describe ecosystem structure and dynamics (Figure 1).

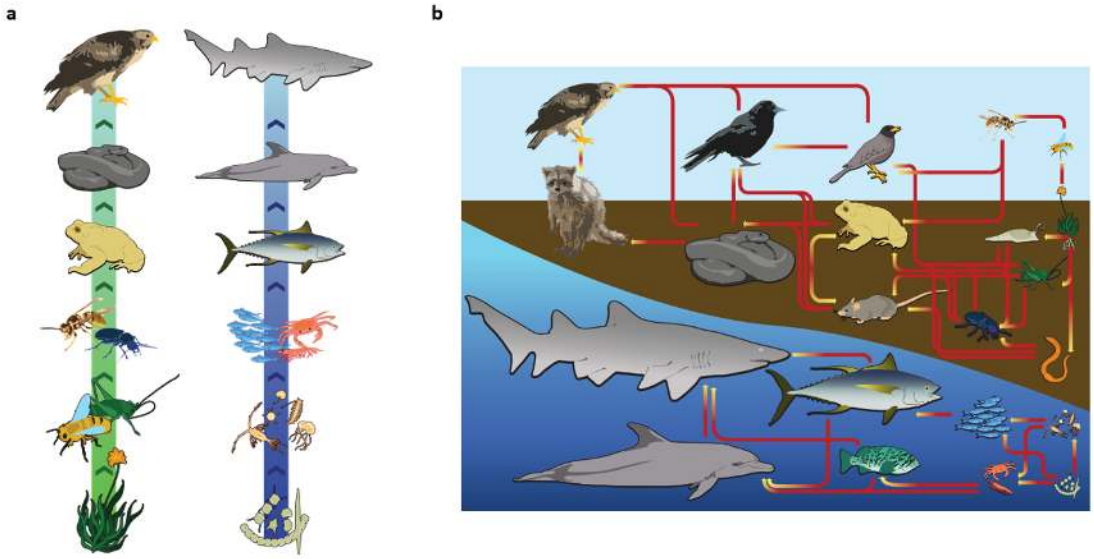


Figure 1. Example of simplified food chains (a) and food webs (b) of terrestrial and marine ecosystems. Developed by LadyofHats and licensed under CC0.

Though more complex than a food chain, a food web remains a simplified illustration of the direct and indirect trophic interactions among species in an ecosystem. Food webs often aggregate many species into trophic groups, which are functional groups of species that have the same predators and prey in a food web. Software can be used to model more complex interactions (Figure 2), but no food web model can capture all of the complexity found within a natural ecosystem.

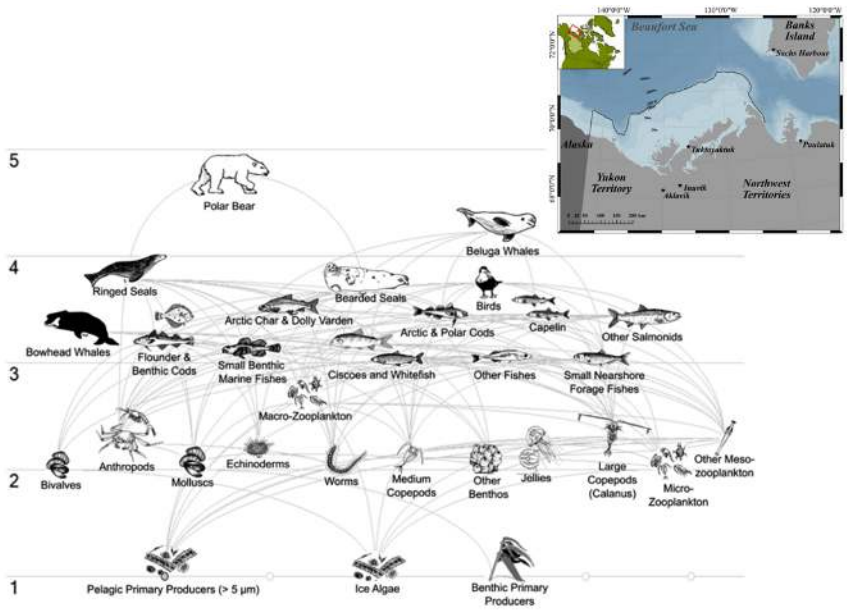
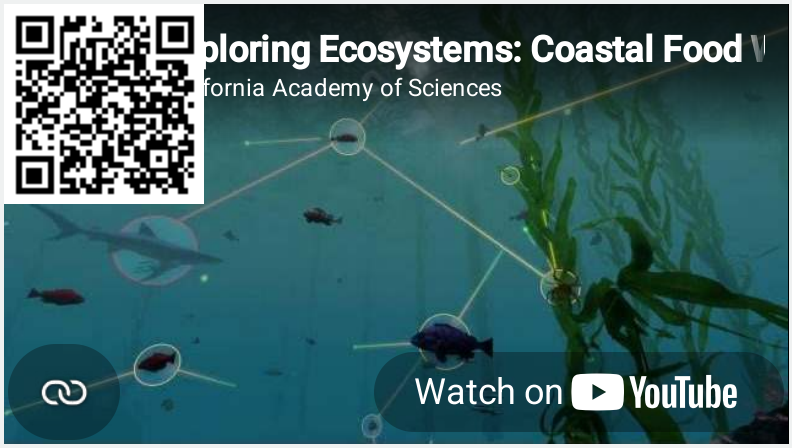


Figure 2: An example of a more complex food web developed by Hoover et al. 2021 using a program called Ecopath. This food web depicts trophic relationships among species in the Canadian Beaufort Sea. Horizontal lines represent trophic level. Image licensed under CC-BY 4.0.

Video



Components of a Food Web

The three basic ways in which organisms get food are as producers, consumers, and decomposers.

- Producers (autotrophs) are typically plants or algae. Plants and algae do not usually eat other organisms, but pull nutrients from the soil or the ocean and manufacture their own food using photosynthesis. For this reason, they are called primary producers. In this way, it is energy from the sun that usually powers the base of the food chain (Cengage Learning 2002). An exception occurs in deep-sea hydrothermal ecosystems, where there is no sunlight. Here primary producers manufacture food through a process called chemosynthesis (van Dover 2000).
- Consumers (heterotrophs) are species that cannot manufacture their own food and need to consume other organisms. Animals that eat primary producers (like plants) are called herbivores. Animals that eat other animals are called carnivores, and animals that eat both plants and other animals are called omnivores.

- Decomposers (detritivores) break down dead plant and animal material and wastes and release it again as energy and nutrients into the ecosystem for recycling. Decomposers, such as bacteria and fungi (mushrooms), feed on waste and dead matter, converting it into inorganic chemicals that can be recycled as mineral nutrients for plants to use again.

Autotrophs

Energy is acquired by living things in three ways: photosynthesis, chemosynthesis, and the consumption and digestion of other living or previously living organisms by heterotrophs.

Photosynthetic and chemosynthetic organisms are both grouped into a category known as **autotrophs**: organisms capable of synthesizing their own food (more specifically, capable of using inorganic carbon as a carbon source). Photosynthetic autotrophs (**photoautotrophs**) use sunlight as an energy source, whereas chemosynthetic autotrophs (**chemoautotrophs**) use inorganic molecules as an energy source. Autotrophs are critical for all ecosystems. Without these organisms, energy would not be available to other living organisms and life itself would not be possible.

Photoautotrophs, such as plants, algae, and photosynthetic bacteria, serve as the energy source for a majority of the world's ecosystems. Photoautotrophs harness the solar energy of the sun by converting it to chemical energy in the form of ATP (and NADP). The energy stored in ATP is used to synthesize complex organic molecules, such as glucose.

Chemoautotrophs are primarily bacteria that are found in rare ecosystems where sunlight is not available, such as in those associated with dark caves or hydrothermal vents at the bottom of the ocean (Figure 3). Many chemoautotrophs in hydrothermal vents use hydrogen sulfide (H2S), which is released from the vents as a source of chemical energy. This allows chemoautotrophs to synthesize complex organic molecules, such as glucose, for their own energy and in turn supplies energy to the rest of the ecosystem.

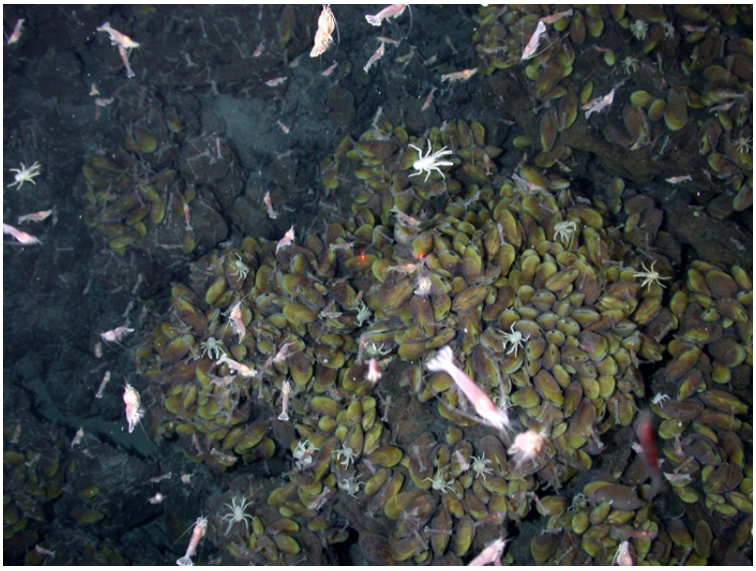
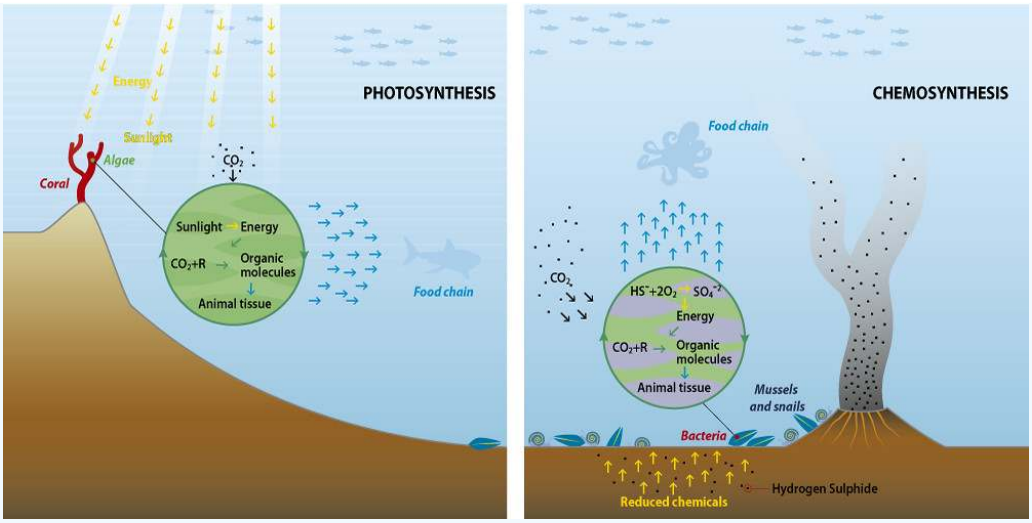


Figure 3 Swimming shrimp, a few squat lobsters, and hundreds of vent mussels are seen at a hydrothermal vent at the bottom of the ocean. As no sunlight penetrates to this depth, the ecosystem is supported by chemoautotrophic bacteria and organic material that sinks from the ocean's surface. This picture was taken in 2006 at the submerged NW Eifuku volcano off the coast of Japan by the National Oceanic and Atmospheric Administration (NOAA). The summit of this highly active volcano lies 1535 m below the surface.

Not Your Average Food Web: Deep Sea 19.1.1

Food webs in the deep sea vary depending on proximity to seamount, hydrothermal vents, and trenches. In areas near hydrothermal vents, chemosynthetic bacteria are the major primary producers. These chemoautotrophs are what provides energy for the rest of the trophic levels in this system.



A comparison of photosynthetic (left) vs. chemosynthetic (right) food webs. Diagram developed by GRID-Arendal and licensed under CC-SA-NC.

Species in deep-sea ecosystems have adapted to interact with each other in many ways. One key interaction is the symbiosis between many species and chemosynthetic bacteria in hydrothermal vent systems. These bacteria live within the body of species like tubeworms, which are dependent on the bacteria to survive, similar to the relationship between zooxanthellae and coral. Another important type of deep sea community develops when a dead whale (or other large marine organism) carcass sinks to the ocean floor and provides an influx of nutrients. The communities support scavengers like hagfish, opportunists like bristle worms, and eventually enter a sulfophilic stage that appears similar to a hydrothermal vent community.



Whale falls serve as an extremely important influx of nutrients to the sun-starved deep ocean. This photo shows a Whale skeleton submerged in Monterey Bay National Marine Sanctuary, covered in octopuses and several other species. Photo by National Marine Sanctuaries is licenced under CC 2.0.

Heterotrophs

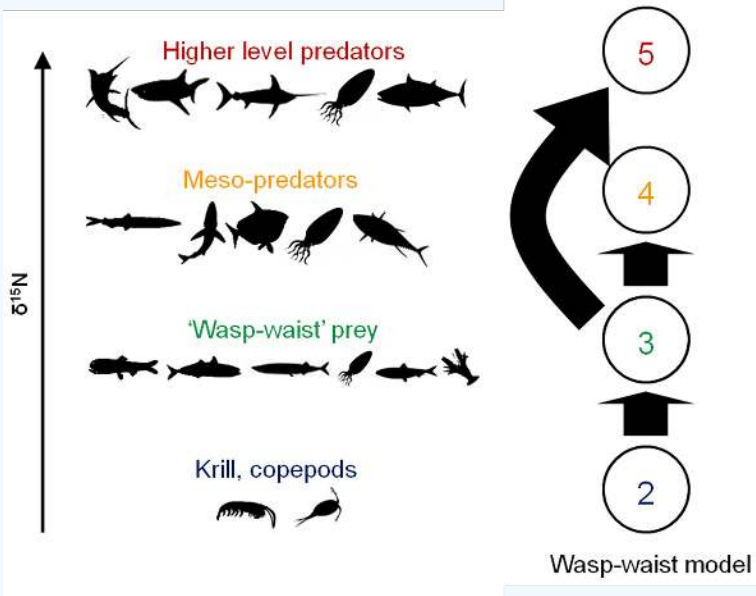
Unlike autotrophs, **heterotrophs** consume rather than produce biomass energy as they metabolize, grow, and add to levels of secondary production. A food web depicts a collection of polyphagous heterotrophic consumers that network and cycle the flow of energy and nutrients from a productive base of self-feeding autotrophs (Pimm et al. 1991; Odum and Barrett 2005; Benke 2010). Autotrophs and heterotrophs come in all sizes, from microscopic to many tonnes - from cyanobacteria to giant redwoods, and from viruses to blue whales.

A gradient exists between trophic levels running from complete autotrophs that obtain their sole source of carbon from the atmosphere, to mixotrophs (such as carnivorous plants) that are autotrophic organisms that partially obtain organic matter from sources other than the atmosphere, and complete heterotrophs that must feed to obtain organic matter.

There are different kinds of feeding relations that can be roughly divided into herbivory, carnivory, scavenging and parasitism. Some of the organic matter eaten by heterotrophs, such as sugars, provides energy. An often overlooked but key component of food webs are the decomposers.

Not Your Average Food Web: Wasp-Waist Ecosystems 19.1.2

Food webs can be controlled by top-down mechanisms (predator abundance determines the abundance of lower trophic levels), bottom-up mechanisms (primary producer abundance determines the abundance of higher trophic levels), or a combination of both. In wasp-waist food webs, population dynamics are controlled by planktivorous lower trophic level species such as sardine, anchovy, and small squids rather than the bottom or the top (Cury et al. 2011). These lower trophic level species often have high abundance but low diversity. The term “wasp-waist” describes the shape of these food webs, with many species existing at lower trophic levels (i.e., the plankton) and at higher trophic level (i.e., the predators), but very few lower trophic level species linking the plankton and the predators. These lower trophic level species exert top-down control on zooplankton and bottom-up control on top predators, with environmental factors largely affecting their abundance (Cury et al. 2000; Cury et al. 2003). Wasp-waist ecosystems are highly vulnerable to collapse when forage fish decline due to the critical energetic links that they provide between highly available zooplankton and larger predators (Shannon 2000).



A diagram showing the structure of a wasp-waist model for the California Current Large Marine Ecosystem. Arrows indicate inputs of a trophic group to another. Figure modified from Madigan et al. 2012.

Decomposers, Detritivores, and Scavangers

Decomposers are organisms that break down dead or decaying organisms; they carry out decomposition, a process possible by only certain kingdoms, such as fungi (NOAA 2014). Like herbivores and predators, decomposers are heterotrophic, meaning that they use organic substrates to get their energy, carbon and nutrients for growth and development.



Figure 4: Fungi are the primary decomposers in most environments, illustrated here *Mycena interrupta*. Only fungi produce the enzymes necessary to decompose lignin, a chemically complex substance found in wood.

Detritivores (also known as **detrivores**, **detritophages**, **detritus feeders**, or **detritus eaters**) are heterotrophs that obtain nutrients by consuming detritus (decomposing plant and animal parts as well as feces) (Wetzel 2001). There are many kinds of invertebrates, vertebrates and plants that carry out coprophagy. By doing so, all these detritivores contribute to decomposition and the nutrient cycles. Detritivores are usually arthropods and help in the process of remineralization.

Plant tissues are made up of resilient molecules (cellulose, chitin, lignin and xylan) that decay at a much lower rate than other organic molecules. Detritivores perform the first stage of remineralization, by fragmenting the dead plant matter, allowing decomposers to perform the second stage of remineralization (Keddy 2017). The activity of detritivores are the reason why we do not see an accumulation of plant litter in nature (Keddy 2017; Sagi et al. 2019).

While the terms decomposer and detritivore are often interchangeably used, detritivores *ingest* and digest dead matter internally, while decomposers *directly absorb* nutrients through external chemical and biological processes (Keddy 2017). Thus, invertebrates such as earthworms, woodlice, and sea cucumbers are technically detritivores, not decomposers, since they must ingest nutrients - they are unable to absorb them externally (Sagi et al. 2019).

Detritivores are an important aspect of many ecosystems. They can live on any type of soil with an organic component, including marine ecosystems, where they are termed interchangeably with bottom feeders. Typical detritivorous animals include millipedes, springtails, woodlice, dung flies, slugs, many terrestrial worms, sea stars, sea cucumbers, fiddler crabs, and some sedentary polychaetes such as worms of the family Terebellidae.

Scavengers are animals that consume dead organisms that have died from causes other than predation or have been killed by other predators (Tan and Corlett 2011). While scavenging generally refers to carnivores feeding on carrion, it is also a herbivorous feeding behavior (Getz 2011). Scavengers play a fundamental role in the environment through the removal of decaying organisms, serving as a natural sanitation service (Ogada et al. 2011). While microscopic and invertebrate decomposers break down dead organisms into simple organic matter which are used by nearby autotrophs, scavengers help conserve energy and nutrients obtained from carrion within the upper trophic levels, and are able to disperse the energy and nutrients farther away from the site of the carrion than decomposers (Olson et a. 2016). Decomposers and detritivores complete this process, by consuming the remains left by scavengers. Scavengers are not typically thought to be detritivores, as they generally eat large quantities of organic matter.

Decomposers are often left off food webs, but if included, they mark the end of a food chain (Hutchinson 2013). Thus food chains start with primary producers and end with decay and decomposers. Since decomposers recycle nutrients, leaving them so they can be reused by primary producers, they are sometimes regarded as occupying their own trophic level (Kane et al. 2016; Pahl and Ruedas 2021).

Not Your Average Food Web: Detrital Web 19.1.3

Detritus is dead particulate organic material, as distinguished from dissolved organic material. Detritus typically includes the bodies or fragments of bodies of dead organisms, and fecal material. Detritus typically hosts communities of microorganisms that colonize and decompose (i.e. remineralize) it. In terrestrial ecosystems it is present as leaf litter and other organic matter that is intermixed with soil, which is denominated "soil organic matter". The detritus of aquatic ecosystems is organic material that is suspended in the water and accumulates in depositions on the floor of the body of water; when this floor is a seabed, such a deposition is denominated "marine snow".



Earthworms are soil-dwelling detritivores.



Two Adonis blue butterflies lap at a small lump of feces lying on a rock.

In a detrital web, plant and animal matter is broken down by decomposers, e.g., bacteria and fungi, and moves to detritivores and then carnivores (Gönenç et al. 2007). There are often relationships between the detrital web and the grazing web. Mushrooms produced by decomposers in the detrital web become a food source for deer, squirrels, and mice in the grazing web. Earthworms are detritivores that consume decaying leaves and are then consumed by a variety of wildlife, especially birds.

Video



Trophic Levels

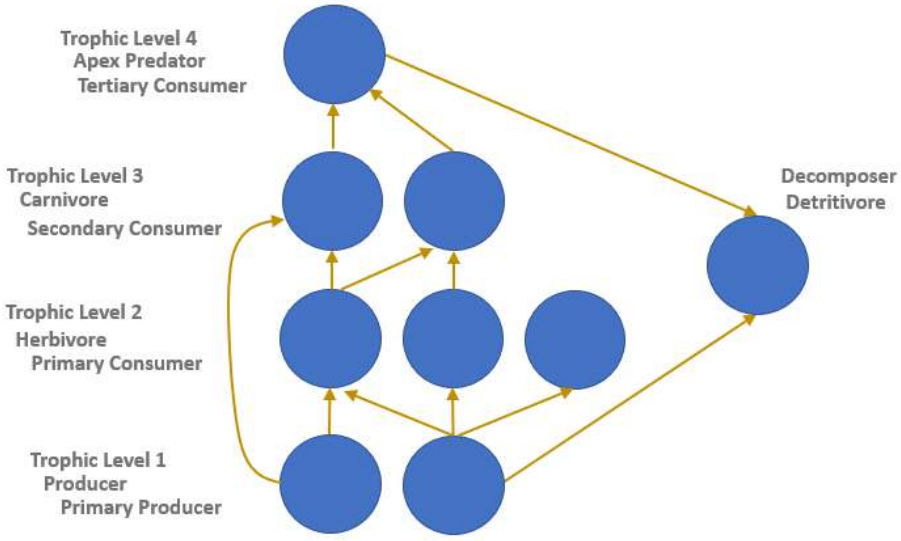


Figure 7: Food web diagram showing the various ways in which organism roles can be differentiated. Developed by N. Gownaris.

The **trophic level** of an organism is the position it occupies in a food web. A food chain is a succession of organisms that eat other organisms and may, in turn, be eaten themselves. The trophic level of an organism is the number of steps it is from the start of the chain. A food web starts at trophic level 1 with primary producers such as plants, can move to herbivores at level 2, carnivores at level 3 or higher, and typically finish with apex predators at level 4 or 5. The path along the chain can form either a one-way flow or a food "web". Ecological communities with higher biodiversity form more complex trophic paths. The word trophic derives from the Greek τροφή (trophē) referring to food or nourishment (merriam-webster.com, 2017).

Trophic levels can be represented by numbers, starting at level 1 with plants. Further trophic levels are numbered subsequently according to how far the organism is along the food chain.

- Level 1: Plants and algae make their own food and are called producers.
- Level 2: Herbivores eat plants and are called primary consumers.
- Level 3: Carnivores that eat herbivores are called secondary consumers.
- Level 4: Carnivores that eat other carnivores are called tertiary consumers.
- Apex predators by definition have no predators and are at the top of their food web.

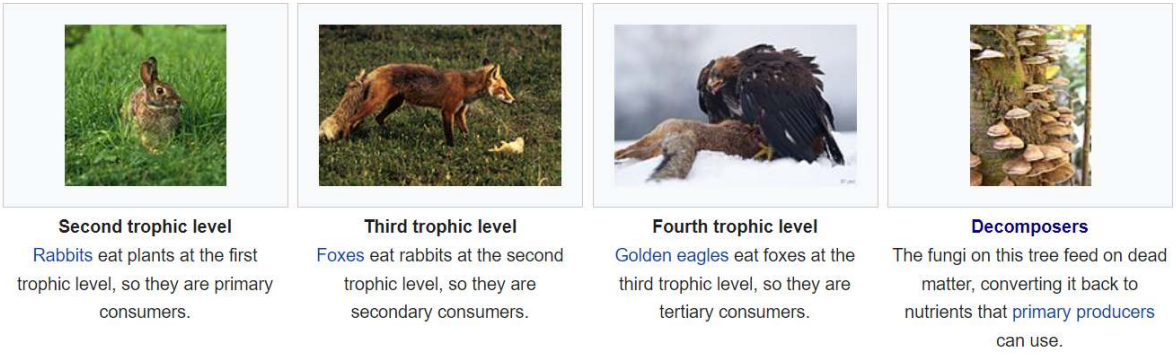


Figure 8: Examples of species found at each trophic level of a terrestrial ecosystem.

The trophic level concept was introduced in a historical landmark paper on trophic dynamics in 1942 by Raymond L. Lindeman. The basis of trophic dynamics is the transfer of energy from one part of the ecosystem to another (Odum and Heald 1975; Cortés 1999). The trophic dynamic concept has served as a useful quantitative heuristic, but it has several major limitations including the precision by which an organism can be allocated to a specific trophic level. Omnivores, for example, are not restricted to any single level. Nonetheless, recent research has found that discrete trophic levels do exist, but "above the herbivore trophic level, food webs are better characterized as a tangled web of omnivores." (Pauly et al. 1998).



Figure 9: Killer whales (orca) are apex predators but they are divided into separate populations that hunt specific prey, such as tuna, small sharks, and seals.

The fisheries scientist Daniel Pauly sets the values of trophic levels to one in plants and detritus, two in herbivores and detritivores (primary consumers), three in secondary consumers, and so on. The definition of the trophic level, TL, for any consumer species is (Pauly and Palomares 2005)

$$TL_i = 1 + \sum_j (TL_j \cdot DC_{ij})$$

where

$$TL_j$$

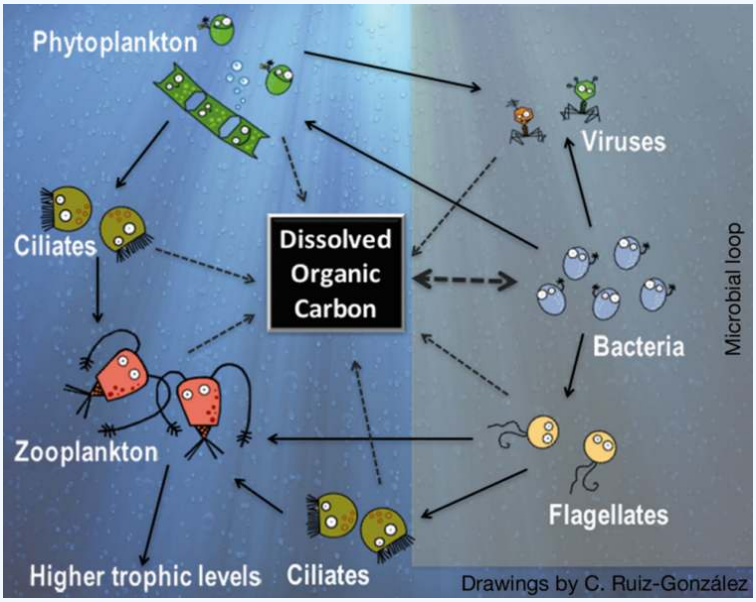
is the fractional trophic level of the prey j, and

$$DC_{ij}$$

represents the fraction of j in the diet of i. That is, the consumer trophic level is one plus the weighted average of how much different trophic levels contribute to its food.

In the case of marine ecosystems, the trophic level of most fish and other marine consumers takes a value between 2.0 and 5.0. The upper value, 5.0, is unusual, even for large fish (Cortés 1999), though it occurs in apex predators of marine mammals, such as polar bears and orcas (Pauly et al. 1998).

Not Your Average Food Web: Microbial Loop 19.1.4



Simplified microbial food web in the sunlit ocean by Anders et al. is licensed under CC-BY-SA 4.0. Left side: classic description of the carbon flow from photosynthetic algae to grazers and higher trophic levels in the food chain. Right side: microbial loop, with bacteria using dissolved organic carbon to gain biomass, which then re-enters the classic carbon flow through protists. Based on DeLong & Karl (2005).

The microbial food web refers to the combined trophic interactions among microbes in aquatic environments. These microbes include viruses, bacteria, algae, heterotrophic protists (such as ciliates and flagellates) (Mostajir et al. 2015). Scientists have relatively recently begun to appreciate the importance of this microscopic food web to the functioning of higher trophic levels.

In aquatic environments, microbes constitute the base of the food web. Single celled photosynthetic organisms such as diatoms and cyanobacteria are generally the most important primary producers in the open ocean. Many of these cells, especially cyanobacteria, are too small to be captured and consumed by small crustaceans and planktonic larvae. Instead, these cells are consumed by phagotrophic protists which are readily consumed by larger organisms. Viruses can infect and break open bacterial cells and (to a lesser extent), planktonic algae (a.k.a. phytoplankton). Therefore, viruses in the microbial food web act to reduce the population of bacteria and, by lysing bacterial cells, release particulate and dissolved organic carbon (DOC). DOC may also be released into the environment by algal cells. The microbial loop describes a pathway in the microbial food web where DOC is returned to higher trophic levels via the incorporation into bacterial biomass.

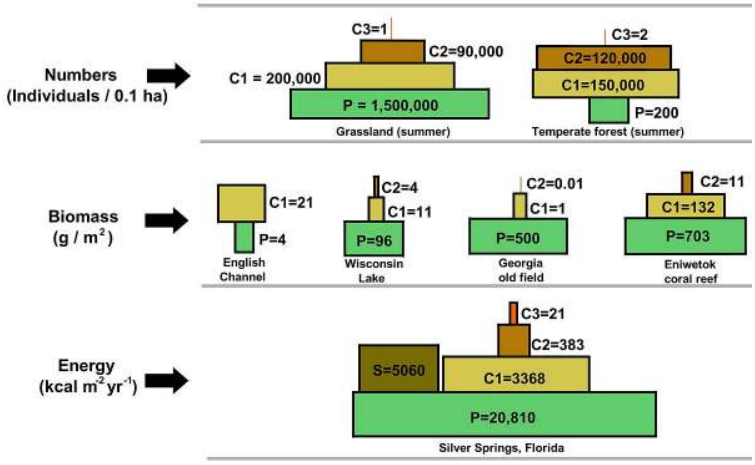


Figure 10: Illustration of a range of ecological pyramids, including **top** pyramid of numbers, **middle** pyramid of biomass, and **bottom** pyramid of energy. The terrestrial forest (summer) and the English Channel ecosystems exhibit inverted pyramids.*Note:* trophic levels are not drawn to scale and the pyramid of numbers excludes microorganisms and soil animals. *Abbreviations:* P=Producers, C1=Primary consumers, C2=Secondary consumers, C3=Tertiary consumers, S=Saprotrophs (Odum and Barrett 2005).

Ecological trophic pyramids are typically one of three kinds: 1) pyramid of numbers, 2) pyramid of biomass, or 3) pyramid of energy (Odum and Barrett 2005). In a pyramid of numbers, the number of consumers at each level decreases significantly, so that a single top consumer, (e.g., a polar bear or a human), will be supported by a much larger number of separate producers. There is usually a maximum of four or five links in a food chain, although food chains in aquatic ecosystems are more often longer than those on land. Eventually, all the energy in a food chain is dispersed as heat (Odum and Barrett 2005).

Ecological pyramids place the primary producers at the base. They can depict different numerical properties of ecosystems, including numbers of individuals per unit of area, biomass (g/m2), and energy (k cal m−2 yr−1). The emergent pyramidal arrangement of trophic levels with amounts of energy transfer decreasing as species become further removed from the source of production is one of several patterns that is repeated amongst the planet's ecosystems (Pimm et al. 1991; Raffaelli 2002; Proulx et al. 2005). The size of each level in the pyramid generally represents biomass, which can be measured as the dry weight of an organism (Rickleffs 1996). Autotrophs may have the highest global proportion of biomass, but they are closely rivaled or surpassed by microbes (Whitman et al. 1998; Grommbridge and Jenkins 2002).

Pyramid structure can vary across ecosystems and across time. In some instances biomass pyramids can be inverted. This pattern is often identified in aquatic and coral reef ecosystems. The pattern of biomass inversion is attributed to different sizes of producers. Aquatic communities are often dominated by producers that are smaller than the consumers that have high growth rates. Aquatic producers, such as planktonic algae or aquatic plants, lack the large accumulation of secondary growth as exists in the woody trees of terrestrial ecosystems. However, they are able to reproduce quickly enough to support a larger biomass of grazers. This inverts the pyramid. Primary consumers have longer lifespans and slower growth rates that accumulate more biomass than the producers they consume. Phytoplankton live just a few days, whereas the zooplankton eating the phytoplankton live for several weeks and the fish eating the zooplankton live for several consecutive years (Spellman 2008). Aquatic predators also tend to have a lower death rate than the smaller consumers, which contributes to the inverted pyramidal pattern. Population structure, migration rates, and environmental refuge for prey are other possible causes for pyramids with biomass inverted. Energy pyramids, however, will always have an upright pyramid shape if all sources of food energy are included and this is dictated by the second law of thermodynamics (Odum and Barrett 2005; Wang et al. 2009).

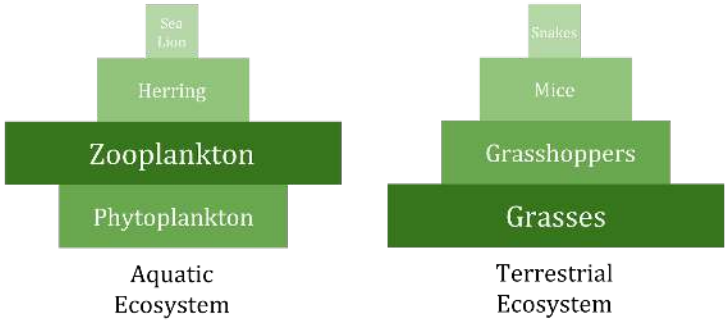
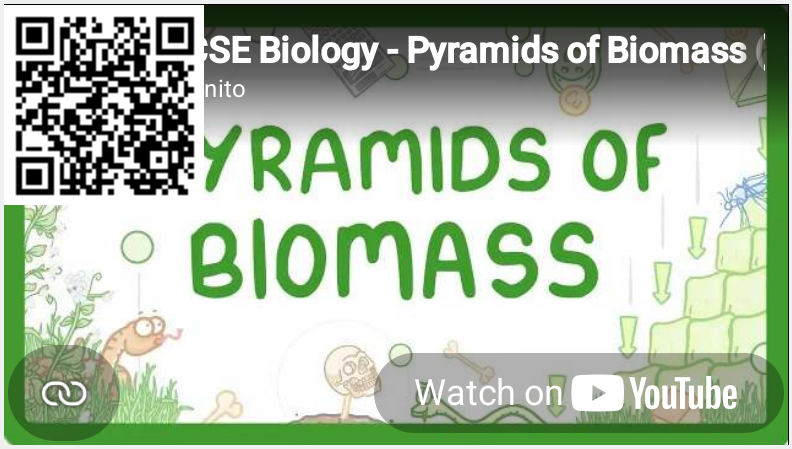


Figure 11: A pyramid of biomass shows the total biomass of the organisms involved at each trophic level of an ecosystem. These pyramids are not necessarily upright. There can be lower amounts of biomass at the bottom of the pyramid if the rate of primary production per unit biomass is high.

Video



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19.2: Quantifying Food Webs

Ecologists collect data on trophic levels and food webs to statistically model and mathematically calculate parameters, such as those used in other kinds of network analysis (e.g., graph theory), to study emergent patterns and properties shared among ecosystems. There are different ecological dimensions that can be mapped to create more complicated food webs, including: species composition (type of species), richness (number of species), biomass (the dry weight of plants and animals), productivity (rates of conversion of energy and nutrients into growth), and stability (food webs over time). A food web diagram illustrating species composition shows how change in a single species can directly and indirectly influence many others. The sections below describe three metrics that ecologists use to describe and quantify food webs (Transfer Efficiency, Food Chain Length, Connectance).

Transfer Efficiency

The biomass of each trophic level decreases from the base of the chain to the top. This is because energy is lost to the environment with each transfer as entropy increases. About eighty to ninety percent of the energy is expended for the organism's life processes or is lost as heat or waste. Only about ten to twenty percent of the organism's energy is generally passed to the next organism (Spellman, 2008). The amount can be less than one percent in animals consuming less digestible plants, and it can be as high as forty percent in zooplankton consuming phytoplankton (Kent, 2000). Graphic representations of the biomass or productivity at each trophic level are called ecological pyramids or trophic pyramids. The proportion of energy that is transferred from one trophic level to the next is known as the **transfer efficiency** of a food web.

The **ten percent law** of transfer of energy from one trophic level to the next can be attributed to Raymond Lindeman (1942) (Odum & Barrett, 2005). However, Lindeman did not call it a "law" and cited transfer efficiencies ranging from 0.1% to 37.5%. According to this law, during the transfer of organic food energy from one trophic level to the next higher level, only about ten percent of the transferred energy is stored as flesh. The remaining is lost during transfer, broken down in respiration, or lost to incomplete digestion by higher trophic level.

When organisms are consumed, approximately 10% of the energy in the food is fixed into their flesh and is available for the next trophic level (carnivores or omnivores). When a carnivore or an omnivore in turn consumes that animal, only about 10% of energy is fixed in its flesh for the higher level. Again, it is important to remember that the 10% value represents an estimate and that, in reality, transfer efficiency varies highly among ecosystems, time periods, and trophic levels.

Example: The Sun releases 10,000 J of energy, then plants take only 100 J of energy from sunlight (this is an exception to the 10% rule, since only 1% of energy is taken up by plants from sun); thereafter, a deer would take 10 J (10% of energy) from the plant. A wolf eating the deer would only take 1 J (10% of energy from deer). A human eating the wolf would take 0.1J (10% of energy from wolf), etc.

The ten percent law provides a basic understanding on the cycling of food chains. Furthermore, the ten percent law shows the inefficiency of energy capture at each successive trophic level. The rational conclusion is that energy efficiency is best preserved by sourcing food as close to the initial energy source as possible.

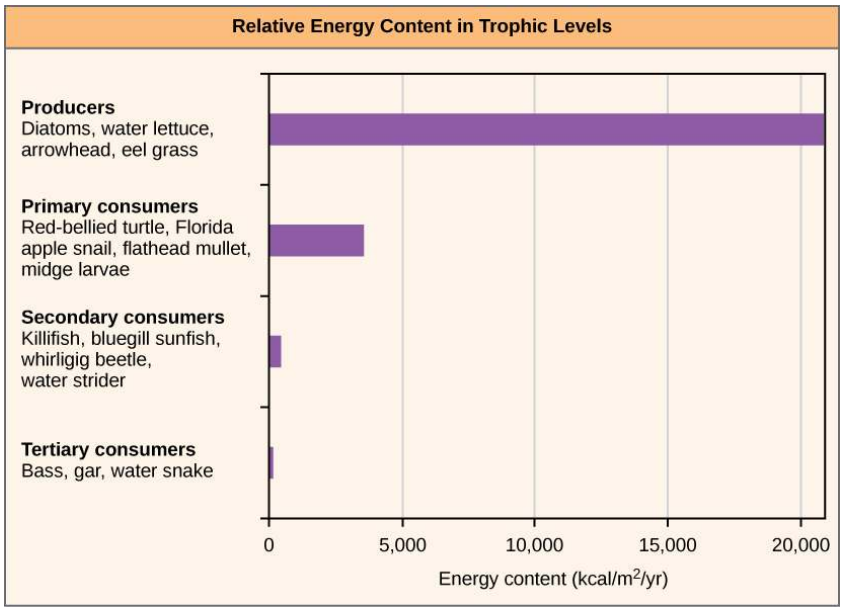


Figure 19.2.1**:** The relative energy in trophic levels in a Silver Springs, Florida, ecosystem is shown. Each trophic level has less energy available, and usually, but not always, supports a smaller mass of organisms at the next level.

Food Chain Length

A common metric used to quantify food web trophic structure is food chain length. Food chain length is another way of describing food webs as a measure of the number of species encountered as energy or nutrients move from the plants to top predators (Post, 1993). In its simplest form, the length of a chain is the number of links between a trophic consumer and the base of the web or the maximum trophic level of a species in that food web. The mean chain length of an entire web is the arithmetic average of the lengths of all chains in a food web (Pimm, 1979; Odum & Barrett, 2005). In a simple predator-prey example, a deer is one step removed from the plants it eats (chain length = 1) and a wolf that eats the deer is two steps removed from the plants (chain length = 2). Because energy is lost at each transfer from one trophic level to the next (see Transfer Efficiency), the maximum number of trophic levels is generally constrained to only four or five levels. The number of trophic levels is ultimately determined by the productivity at the base of the food web and by how efficiently this energy is transferred up the food chain. Greater productivity and higher efficiency can support a greater number of trophic levels.

Connectance

Food webs are extremely complex. Complexity is a measure of an increasing number of permutations and it is also a metaphorical term that conveys the mental intractability or limits concerning unlimited algorithmic possibilities. In food web terminology, complexity is a product of the number of species and connectance (Neutel et al., 2002; Leveque, 2003; Proctor et al., 2005). Connectance is "the fraction of all possible links that are realized in a network" (Dunne et al., 2002). These concepts were derived and stimulated through the suggestion that complexity leads to stability in food webs, such as increasing the number of trophic levels in more species rich ecosystems. This hypothesis was challenged through mathematical models suggesting otherwise, but subsequent studies have shown that the premise holds in real systems (Neutel et al., 2002; Banasek-Richter et al., 2009).

While the complexity of real food webs connections are difficult to decipher, ecologists have found mathematical models on networks an invaluable tool for gaining insight into the structure, stability, and laws of food web behaviors relative to observable outcomes. Quantitative formulas simplify the complexity of food web structure. The number of trophic links (tL), for example, is converted into a connectance value:

$$C = L/[S(S-1)/2]$$

where, S(S-1)/2 is the maximum number of binary connections among S species (Paine 1988). "Connectance (C) is the fraction of all possible links that are realized (L/S2) and represents a standard measure of food web complexity..." (Williams et al., 2002).

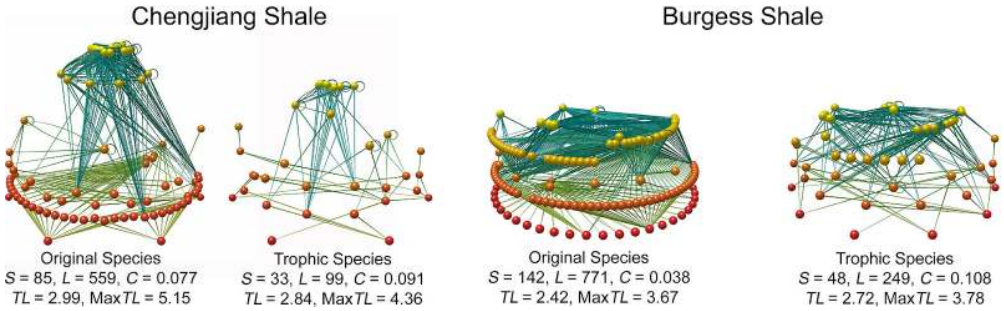


Figure 19.2.2**:** Food web and trophic level of the Chengjiang and Burgess Shale. S: number of species (nodes). L: number of trophic links. C: connectance; L/S2. MaxTL: maximum trophic level of a species in the web. Paleoecological studies can reconstruct fossil food-webs and trophic levels. Primary producers form the base (red spheres), predators at top (yellow spheres), the lines represent feeding links. Original food-webs (left) are simplified (right) by aggregating groups feeding on common prey into coarser grained trophic species (Dunne et al., 2008). Figure developed by Dunne et al. 2008 is licensed under CC-BY 4.0.

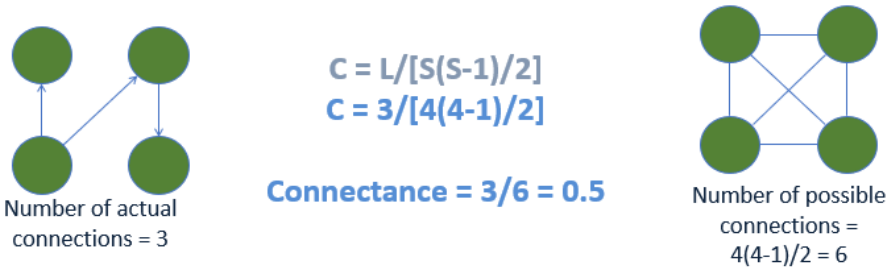


Figure 19.2.3**:** Worked example of calculating connectance for a food web. Diagram by N. Gownaris and A. Wilson.

Techniques for Studying Food Webs 19.2.1

Food web linkages, or the feeding relationships between species inhabiting a shared ecosystem, are an ecological lens through which ecosystem structure and function can be assessed, and thus are fundamental to informing sustainable resource management. Empirical feeding datasets have traditionally been painstakingly generated from stomach content analysis, direct observations and from biochemical trophic markers (stable isotopes, fatty acids, molecular tools). Each approach carries inherent biases and limitations, as well as advantages.

Traditional Approaches to Studying Food Webs

Traditional approaches to food web analysis include gut and scat content analysis. In these analyses, the diet of species is determined based on the remains of prey found in their stomachs or in their feces. These approaches are limited because they only allow researchers to examine the hard parts or otherwise undigested components of prey (e.g., otoliths, or ear bones, of fish and teeth of mice). Over the past two decades, stable isotope analysis has become an increasingly common approach to studying food webs. Even more recently, two new methods to studying food webs have emerged: the use of remotely operated

vehicles and the use of DNA in feces and gut contents. Below, we provide an example of a recent study using remotely operated vehicles to study food webs and diet in the deep sea.



Figure 19.2.4**:** Traditional food web analysis has often entailed gut content analysis or fecal content analysis. Scientists use the bits of prey that remain to calculate estimates of variables like percent occurrence for each prey type. The top photo (taken by N. Gownaris, licenced CC-BY) shows a tilapia in the stomach of a Nile perch; very rarely is gut content analysis this straightforward! The bottom photo (inside the owl pellet by Art Siegel and licensed under CC-BY-NC 2.0) shows prey remains removed from an owl pellet, including teeth, claws, and bones of owl prey.

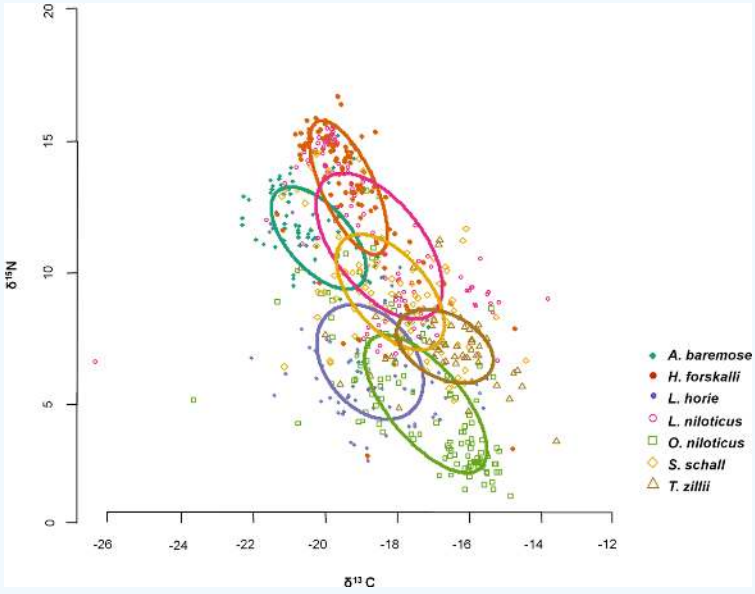


Figure 19.2.5**:** An example of a food web study using stable isotopes of seven key fish species in Lake Turkana, Kenya. In stable isotope studies, δ13C provides information on the foraging habitat of each species, while δ15N provides information on the trophic level. Species foraging more offshore or more pelagically have a lower δ13C signature and species feeding at lower trophic levels have a lower δ15N signature. In this example, *H. forskalii* is a pelagic fish (i.e., it feeds in the lake's open waters) and has the highest trophic level among the species studied. Figure from Gownaris et al., 2015.

The Use of Remotely Operated Vehicles to Understand Understudied Food Webs

Within the deep sea, Earth's largest ecosystem, the challenge of gathering empirical feeding data for food webs is particularly formidable due to logistical access and sampling constraints (Robison, 2004). Analyzing the contents of a consumer's stomach (gut or stomach content analysis) is the common and most directly quantitative way of inferring diet, and is an irreplaceable approach for determining the taxonomic identity of food web components. However, for deeper-dwelling fishes with internal gas spaces, stomach eversion can confound this approach (Drazen & Sutton, 2017). These analyses may also fail to quantify gelatinous prey that are readily digested and become quickly unrecognizable (Hyslop, 1980; Choy, 2013).

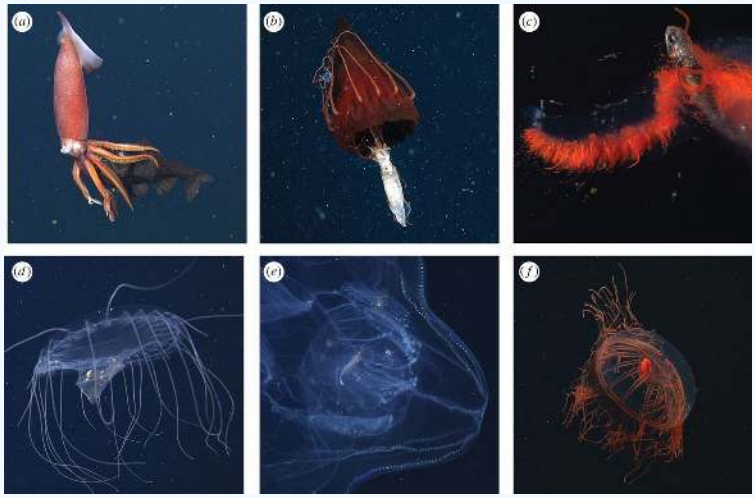


Figure 19.2.6**:** A suite of six illustrative ROV frame grabs of pelagic predators and their prey included in Choy et al. (2017). No scale bars for size are available from these sequences. From left to right, top to bottom: (a) *Gonatus sp.* (squid) feeding on a bathylagid fish (Bathylagidae); (b) *Periphylla periphylla*, the helmet jellyfish, feeding on a gonatid squid (Gonatidae), with a small narcomedusa (*Aegina sp.*) also captured; (c) an undescribed physonect siphonophore known as 'the galaxy siphonophore' feeding on a lanternfish of the family Myctophidae; (d) a narcomedusa, *Solmissus*, ingesting a salp chain (Salpida); (e) the ctenophore *Thalassocalyce inconstans*, with a euphausiid (Euphausiacea) in its gut; and (f) the trachymedusa, *Halitrephes maasi*, with a large, red mysid (Mysidae) in its gut. Figure from Choy et al., 2017.

Choy et al. (2017) used 27 years (1991–2016) of *in situ* feeding observations collected by remotely operated vehicles (ROVs) to quantitatively characterize the deep pelagic food web of central California within the California Current, complementing existing studies of diet and trophic interactions with a unique perspective. Seven hundred and forty-three independent feeding events were observed with ROVs from near-surface waters down to depths approaching 4000 m, involving an assemblage of 84 different predators and 82 different prey types, for a total of 242 unique feeding relationships. The greatest diversity of prey was consumed by narcomedusae, followed by physonect siphonophores, ctenophores and cephalopods. This study highlighted key interactions within the poorly understood 'jelly web', showing the importance of medusae, ctenophores and siphonophores as key predators, whose ecological significance is comparable to large fish and squid species within the central California deep pelagic food web.

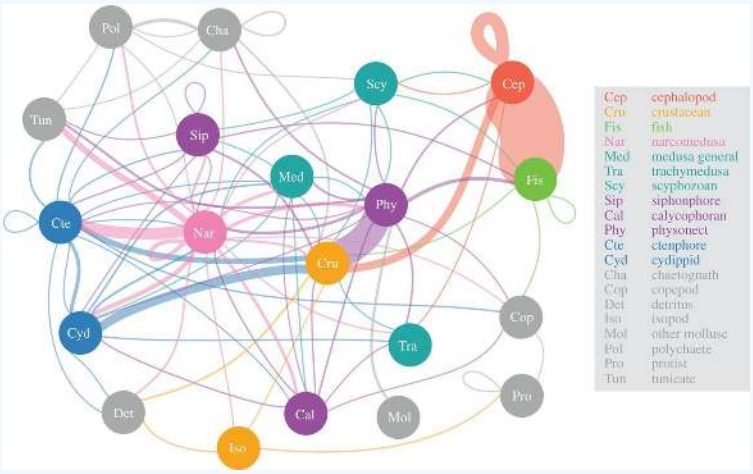


Figure 19.2.7**:** An *in situ* perspective of the food web derived from ROV-based observations of feeding, as represented by 20 broad taxonomic groupings. The linkages between predator to prey are coloured according to predator group origin, and loops indicate within-group feeding. The thickness of the lines or edges connecting food web components is scaled to the log of the number of unique ROV feeding observations across the years 1991–2016 between the two groups of animals. The different groups have eight colour-coded types according to main animal types as indicated by the legend and defined here: red, cephalopods; orange, crustaceans; light green, fish; dark green, medusa; purple, siphonophores; blue, ctenophores and grey, all other animals. In this plot, the vertical axis does not correspond to trophic level, because this metric is not readily estimated for all members. Note that for the Sip and Med groups, there are overlapping sub-groups (calycophoran and physonect siphonophores, and trachymedusa and scyphozoan medusa, respectively), which is attributed to varying levels of taxonomic discrimination possible from *in situ* video observations. Figure from Choy et al., 2017.

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19.3: Trophic Cascades

Introduction

Trophic cascades are powerful indirect interactions that can control entire ecosystems, occurring when a trophic level in a food web is suppressed. For example, a top-down cascade will occur if predators are effective enough in predation to reduce the abundance, or alter the behavior of their prey, thereby releasing the next lower trophic level from predation (or herbivory if the intermediate trophic level is a herbivore).

The trophic cascade is an ecological concept which has stimulated new research in many areas of ecology. For example, it can be important for understanding the knock-on effects of removing top predators from food webs, as humans have done in many places through hunting and fishing.

Top-Down Cascades

A **top-down cascade** is a trophic cascade where the top consumer/predator controls the primary consumer population. In turn, the primary producer population thrives. The removal of the top predator can alter the food web dynamics. In this case, the primary consumers would overpopulate and exploit the primary producers. Eventually there would not be enough primary producers to sustain the consumer population. Top-down food web stability depends on competition and predation in the higher trophic levels. Invasive species can also alter this cascade by removing or becoming a top predator. This interaction may not always be negative. Studies have shown that certain invasive species have begun to shift cascades; and as a consequence, ecosystem degradation has been repaired (Kotta et al. 2018; Megrey and Werner).

These trophic interactions shape patterns of biodiversity globally. Humans and climate change have affected these cascades drastically. One example can be seen with sea otters (Enhydra lutris) on the Pacific coast of the United States of America. Over time, human interactions caused a removal of sea otters. One of their main prey, the pacific purple sea urchin (Strongylocentrotus purpuratus) eventually began to overpopulate. The overpopulation caused increased predation of giant kelp (*Macrocystis pyrifera*). As a result, there was extreme deterioration of the kelp forests along the California coast. This is why it is important for countries to regulate marine and terrestrial ecosystems (Zhang et al. 2018).

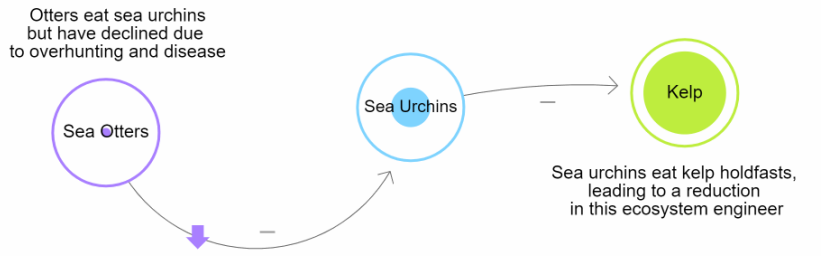


Figure 1: Diagram representing the trophic cascade that occurs when sea otters are removed from coastal marine ecosystems in California, ultimately driving a reduction in habitat due to the loss of Kelp. Developed by N. Gownaris using loopy. Create your own here! LOOPY: a tool for thinking in systems (ncase.me)

Predator-induced interactions could heavily influence the flux of atmospheric carbon if managed on a global scale. For example, a study was conducted to determine the cost of potential stored carbon in living kelp biomass in sea otter (*Enhydra lutris*) enhanced ecosystems. The study valued the potential storage between $205 million and $408 million dollars (US) on the European Carbon Exchange (2012) (Wilmers et al. 2012).

Classic Examples of Trophic Cascades

The earliest empirical demonstrations of trophic cascades came from marine and, especially, aquatic ecosystems. Some of the most famous examples are:

- In North American lakes, piscivorous fish can dramatically reduce populations of zooplanktivorous fish; zooplanktivorous fish can dramatically alter freshwater zooplankton communities, and zooplankton grazing can in turn have large impacts on phytoplankton communities. Removal of piscivorous fish can change lake water from clear to green by allowing phytoplankton to flourish (Carpenter et al. 1985).
- In the Eel River, in Northern California, fish (steelhead and roach) consume fish larvae and predatory insects. These smaller predators prey on midge larvae, which feed on algae. Removal of the larger fish increases the abundance of algae (Power 1990).
- In Pacific kelp forests, sea otters feed on sea urchins. In areas where sea otters have been hunted to extinction, sea urchins increase in abundance and kelp populations are reduced (Estes and Palmisano 1974; Szpak et al. 2013)

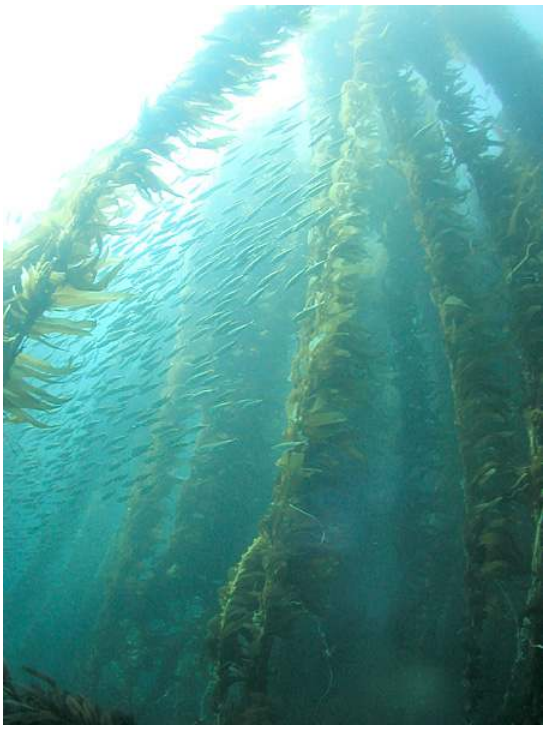


Figure 2: Healthy Pacific kelp forests, like this one at San Clemente Island of California's Channel Islands, have been shown to flourish when sea otters are present. When otters are absent, sea urchin populations can irrupt and severely degrade the kelp forest ecosystem.

Marine Ecosystems

More recent examples of trophic cascades in marine ecosystems have been identified:

- An example of a cascade in a complex, open-ocean ecosystem occurred in the northwest Atlantic during the 1980s and 1990s. The removal of Atlantic cod (*Gadus morhua*) and other ground fishes by sustained overfishing resulted in increases in the abundance of the prey species for these ground fishes, particularly smaller forage fishes and invertebrates such as the northern snow crab (*Chionoecetes opilio*) and northern shrimp (*Pandalus borealis*). The increased abundance of these prey species altered the community of zooplankton that serve as food for smaller fishes and invertebrates as an indirect effect (Frank et al. 2005).
- A similar cascade, also involving the Atlantic cod, occurred in the Baltic Sea at the end of the 1980s. After a decline in Atlantic cod, the abundance of its main prey, the sprat (*Sprattus sprattus*), increased (Alheit et al. 2005) and the Baltic Sea ecosystem shifted from being dominated by cod into being dominated by sprat. The next level of trophic cascade was a decrease in the abundance of *Pseudocalanus acuspes* (Mollmann et al. 2008), a copepod which the sprat prey on.
- On Caribbean coral reefs, several species of angelfishes and parrotfishes eat species of sponges that lack chemical defenses. Removal of these sponge-eating fish species from reefs by fish-trapping and netting has resulted in a shift in the sponge community toward fast-growing sponge species that lack chemical defenses (Loh and Pawlik 2014). These fast-growing sponge

species are superior competitors for space, and overgrow and smother reef-building corals to a greater extent on overfished reefs (Loh et al. 2015).

The fact that the earliest documented trophic cascades all occurred in lakes and streams led a scientist to speculate that fundamental differences between aquatic and terrestrial food webs made trophic cascades primarily an aquatic phenomenon. Trophic cascades were restricted to communities with relatively low species diversity, in which a small number of species could have overwhelming influence and the food web could operate as a linear food chain. Additionally, well-documented trophic cascades at that point in time all occurred in food chains with algae as the primary producer. Trophic cascades, Strong argued, may only occur in communities with fast-growing producers which lack defenses against herbivory.

Terrestrial Examples

Subsequent research has documented trophic cascades in terrestrial ecosystems, including:

- A classic example of a terrestrial trophic cascade is the reintroduction of gray wolves (*Canis lupus*) to Yellowstone National Park, which reduced the number, and changed the behavior, of elk (*Cervus canadensis*). This in turn released several plant species from grazing pressure and subsequently led to the transformation of riparian ecosystems. This example of a trophic cascade is vividly shown and explained in the viral video "How Wolves Change Rivers" (Sustainable Human 2014).
- In the coastal prairie of Northern California, yellow bush lupines are fed upon by a particularly destructive herbivore, the root-boring caterpillar of the ghost moth. Entomopathogenic nematodes kill the caterpillars, and can increase the survival and seed production of lupines (Strong et al. 1999; Preisser 2003).
- In Costa Rican rain forest, a clerid beetle specializes in eating ants. The ant *Pheidole bicornis* has a mutualistic association with *Piper* plants: the ant lives on the *Piper* and removes caterpillars and other insect herbivores. The clerid beetle, by reducing the abundance of ants, increases the leaf area removed from *Piper* plants by insect herbivores (Letourneau and Dyer 1998).

Critics pointed out that published terrestrial trophic cascades generally involved smaller subsets of the food web (often only a single plant species). This was quite different from aquatic trophic cascades, in which the biomass of producers as a whole were reduced when predators were removed. Additionally, most terrestrial trophic cascades did not demonstrate reduced plant biomass when predators were removed, but only increased plant damage from herbivores (Polis et al. 2000). It was unclear if such damage would actually result in reduced plant biomass or abundance.

In 2002 a meta-analysis found trophic cascades to be generally *weaker* in terrestrial ecosystems, meaning that changes in predator biomass resulted in smaller changes in plant biomass (Shurin et al. 2002). In contrast, a study published in 2009 demonstrated that multiple species of trees with highly varying autecologies are in fact heavily impacted by the loss of an apex predator (Beschta and Ripple 2009). Another study, published in 2011, demonstrated that the loss of large terrestrial predators also significantly degrades the integrity of river and stream systems, impacting their morphology, hydrology, and associated biological communities (Beschta and Ripple 2011).

Video



An Ecosystem-Wide Trophic Cascade: The Wolves of Yellowstone National Park

The critics' model is challenged by studies accumulating since the reintroduction of gray wolves (*Canis lupus*) to Yellowstone National Park. The gray wolf, after being extirpated in the 1920s and absent for 70 years, was reintroduced to the park in 1995 and 1996. Since then a three-tiered trophic cascade has been reestablished involving wolves, elk (*Cervus elaphus*), and woody browse species such as aspen (*Populus tremuloides*), cottonwoods (*Populus* spp.), and willows (*Salix* spp.). Mechanisms likely include actual wolf predation of elk, which reduces their numbers, and the threat of predation, which alters elk behavior and feeding habits, resulting in these plant species being released from intensive browsing pressure. Subsequently, their survival and recruitment rates have significantly increased in some places within Yellowstone's northern range. This effect is particularly noted among the range's riparian plant communities, with upland communities only recently beginning to show similar signs of recovery (Ripple and Beschta 2012).

Examples of this phenomenon include:

- A 2–3 fold increase in deciduous woody vegetation cover, mostly of willow, in the Soda Butte Creek area between 1995 and 1999 (Groshong 2004).
- Heights of the tallest willows in the Gallatin River valley increasing from 75 cm to 200 cm between 1998 and 2002 (Ripple and Beschta 2004).
- Heights of the tallest willows in the Blacktail Creek area increased from less than 50 cm to more than 250 cm between 1997 and 2003. Additionally, canopy cover over streams increased significantly, from only 5% to a range of 14–73% (Beschta and Ripple 2007).
- In the northern range, tall deciduous woody vegetation cover increased by 170% between 1991 and 2006 (Baril 2009).
- In the Lamar and Soda Butte Valleys the number of young cottonwood trees that had been successfully recruited went from 0 to 156 between 2001 and 2010 (Ripple and Beschta 2012).

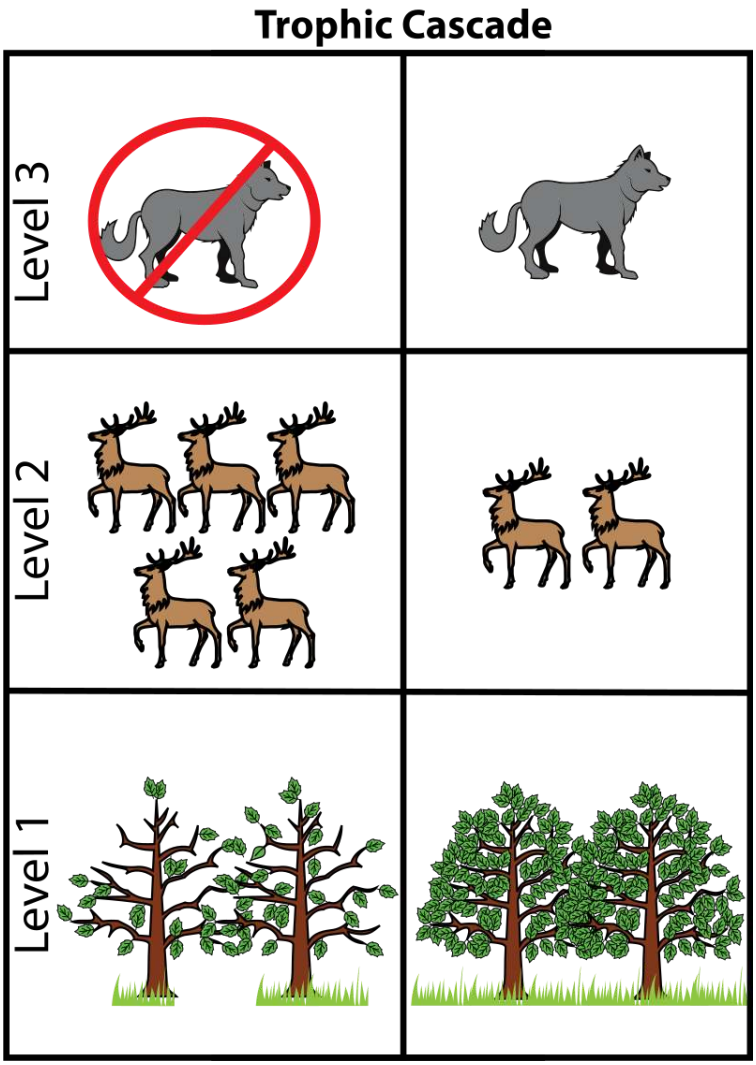


Figure 3: This diagram illustrates trophic cascade caused by removal of the top predator. When the top predator is removed the population of deer is able to grow unchecked and this causes over-consumption of the primary producers.

Trophic cascades also impact the biodiversity of ecosystems, and when examined from that perspective wolves appear to be having multiple, positive cascading impacts on the biodiversity of Yellowstone National Park. These impacts include:

- Scavengers, such as ravens (*Corvus corax*), bald eagles (*Haliaeetus leucocephalus*), and even grizzly bears (*Ursus arctos horribilis*), are likely subsidized by the carcasses of wolf kills (Wilmers et al. 2003).
- In the northern range, the relative abundance of six out of seven native songbirds which utilize willow was found to be greater in areas of willow recovery as opposed to those where willows remained suppressed (Baril 2009).
- Bison (*Bison bison*) numbers in the northern range have been steadily increasing as elk numbers have declined, presumably due to a decrease in interspecific competition between the two species (Painter and Ripple 2012).
- Importantly, the number of beaver (*Castor canadensis*) colonies in the park has increased from one in 1996 to twelve in 2009. The recovery is likely due to the increase in willow availability, as they have been feeding almost exclusively on it. As keystone species, the resurgence of beaver is a critical event for the region. The presence of beavers has been shown to positively impact streambank erosion, sediment retention, water tables, nutrient cycling, and both the diversity and abundance of plant and animal life among riparian communities (Ripple and Beschta 2012).

Video



Other Examples

There are a number of other examples of trophic cascades involving large terrestrial mammals, including:

- In both Zion National Park and Yosemite National Park, the increase in human visitation during the first half of the 20th century was found to correspond to the decline of native cougar (*Puma concolor*) populations in at least part of their range. Soon after, native populations of mule deer (*Odocoileus hemionus*) erupted, subjecting resident communities of cottonwoods (*Populus fremontii*) in Zion and California black oak (*Quercus kelloggii*) in Yosemite to intensified browsing. This halted successful recruitment of these species except in refugia inaccessible to the deer. In Zion the suppression of cottonwoods increased stream erosion and decreased the diversity and abundance of amphibians, reptiles, butterflies, and wildflowers. In parts of the park where cougars were still common these negative impacts were not expressed and riparian communities were significantly healthier (Ripple and Beschta 2006; Ripple and Beschta 2008).
- In sub-Saharan Africa, the decline of lion (*Panthera leo*) and leopard (*Panthera pardus*) populations has led to a rising population of olive baboon (*Papio anubis*). This case of mesopredator release negatively impacted already declining ungulate populations and is one of the reasons for increased conflict between baboons and humans, as the primates raid crops and spread intestinal parasites (Prugh et al. 2009; Estes et al. 2011).
- In the Australian states of New South Wales and South Australia, the presence or absence of dingoes (*Canis lupus dingo*) was found to be inversely related to the abundance of invasive red foxes (*Vulpes vulpes*). In other words, the foxes were most common where the dingoes were least common. Subsequently, populations of an endangered prey species, the dusky hopping mouse (*Notomys fuscus*) were also less abundant where dingoes were absent due to the foxes, which consume the mice, no longer being held in check by the top predator (Letnic and Dworjanyn 2011).

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19.4: References and Attributions

Contributors and Attributions

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- **Energy Flow through Ecosystems (Chapter 46.2) from OpenStaxx Biology 2e**
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CHAPTER OVERVIEW

Chapter 20: Biogeochemical Cycles

Learning Objectives

- Objective 1
- Objective 2
- Objective 3
- Objective 4

20.1: Introduction to Biogeochemical Cycles
20.2: The Biogeochemical Cycles
20.3: Eutrophication and Dead Zones

Summary

Summary to be added

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20.1: Introduction to Biogeochemical Cycles

Learning Objectives

- Summarize the concept of biogeochemical cycles

Key Points

- Carbon, nitrogen, hydrogen, oxygen, phosphorus, and sulfur are conserved and recycled in the atmosphere, on land, in water, or beneath the earth's surface.
- Materials are recycled via erosion, weathering, water drainage, and the movement of tectonic plates.
- Water is essential to all living processes, while carbon is found in all organic macromolecules.
- Nitrogen and phosphorus are major components of nucleic acids and play major roles in agriculture.
- Sulfur plays a role in the three-dimensional folding of proteins and is released into the atmosphere by the burning of fossil fuels.

Key Terms

- **hydrosphere**: combined mass of water found on, under, and over the surface of a planet
- **biogeochemical cycle**: cycling of mineral nutrients through ecosystems and through the non-living world

Introduction

Energy flows directionally through ecosystems, entering as sunlight (or inorganic molecules for chemoautotrophs) and leaving as heat during the many transfers between trophic levels. However, the matter that makes up living organisms is conserved and recycled. The six most common elements associated with organic molecules (carbon, nitrogen, hydrogen, oxygen, phosphorus, and sulfur) take a variety of chemical forms and may exist for long periods in the atmosphere, on land, in water, or beneath the earth's surface. The cycling of these elements is interconnected. Geologic processes, such as weathering, erosion, water drainage, and the movement of the continental plates, all play a role in this recycling of materials. Because geology and chemistry have major roles in the study of this process, the recycling of inorganic matter between living organisms and their environment is called a **biogeochemical cycle**. It is important to remember that while matter and energy are processed in cycles, they aren't necessarily moving in a simple circle and don't really have a beginning or an end. Today, **anthropogenic** (human) activities are altering all major ecosystems and the biogeochemical cycles they drive.

The components of organic molecules are constantly being stored and recycled as part of their biogeochemical cycle. Water, which contains hydrogen and oxygen, is essential to all living processes. The hydrosphere is the area of the earth where water movement and storage occurs. Water can be liquid on the surface and beneath the surface or frozen (rivers, lakes, oceans, groundwater, polar ice caps, and glaciers) or exist as water vapor in the atmosphere. Carbon, found in all organic macromolecules, is an important constituent of fossil fuels. Nitrogen, a major component of our nucleic acids and proteins, is critical to human agriculture. Phosphorus, a major component of nucleic acid (along with nitrogen), is one of the main ingredients in artificial fertilizers used in agriculture and their associated environmental impacts on our surface water. Sulfur, critical to the 3–D folding of proteins (as in disulfide binding), is released into the atmosphere by the burning of fossil fuels, such as coal.

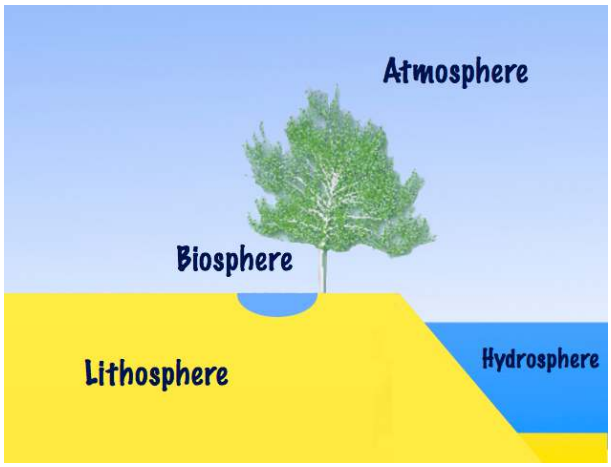


Figure 20.1.1: **Importance of the hydrosphere**: Earth has a hydrosphere, where water movement and storage occurs. It is important for leaching certain components of organic matter into rivers, lakes, and oceans, and is a reservoir for carbon.

The cycling of all of these elements is interconnected. For example, the movement of water is critical for the leaching of nitrogen and phosphate into rivers, lakes, and oceans. Furthermore, the ocean itself is a major reservoir for carbon. Thus, mineral nutrients are cycled, either rapidly or slowly, through the entire biosphere, from one living organism to another, and between the biotic and abiotic world.

What pops into your mind when you hear the word *reservoir*? Probably a body of water, small or large, that is impounded behind a dam. In Earth systems science, the term ***reservoir*** is used for *a distinctive kind of place where a certain kind of material is stored, or resides, for some period of time*. This part of a cycle that holds an element or water for a short period of time is sometimes also called an **exchange pool,** or **pool**. For example, the atmosphere is an exchange pool for water. It usually holds water (in the form of water vapor) for just a few days. Some other examples of reservoirs or pools for water you will encounter in the course include glaciers; the soil layer; the aggregate of bodies of fresh water on the continents (rivers and lakes). Material moves into and out of reservoirs. *The rate at which a given material moves between reservoirs* is called a ***flux***. If the flux of material into and out of a given reservoir is the same for some period of time, that reservoir is said to be in a ***steady state***. Commonly, however, the flux in and the flux out are not equal.

Contributors and Attributions

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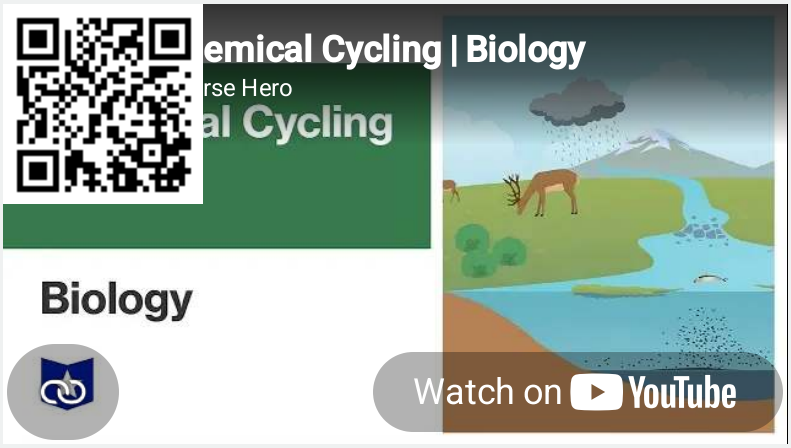
Biogeochemical Cycles

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The cycling of these elements is interconnected. For example, the movement of water is critical for the leaching of nitrogen and phosphate into rivers, lakes, and oceans. Furthermore, the ocean itself is a major reservoir for carbon. Thus, mineral nutrients are cycled, either rapidly or slowly, through the entire biosphere, from one living organism to another, and between the biotic and abiotic world.

Video



The Water (Hydrologic) Cycle

Water is the basis of all living processes. The human body is more than 1/2 water and human cells are more than 70 percent water. Thus, most land animals need a supply of fresh water to survive. However, when examining the stores of water on Earth, 97.5 percent of it is non-potable salt water (Figure 20.2.1). Of the remaining water, 99 percent is locked underground as water or as ice. Thus, less than 1 percent of fresh water is easily accessible from lakes and rivers. Many living things, such as plants, animals, and fungi, are dependent on the small amount of fresh surface water supply, a lack of which can have massive effects on ecosystem dynamics. Humans, of course, have developed technologies to increase water availability, such as digging wells to harvest groundwater, storing rainwater, and using desalination to obtain drinkable water from the ocean. Although this pursuit of drinkable water has been ongoing throughout human history, the supply of fresh water is still a major issue in modern times.

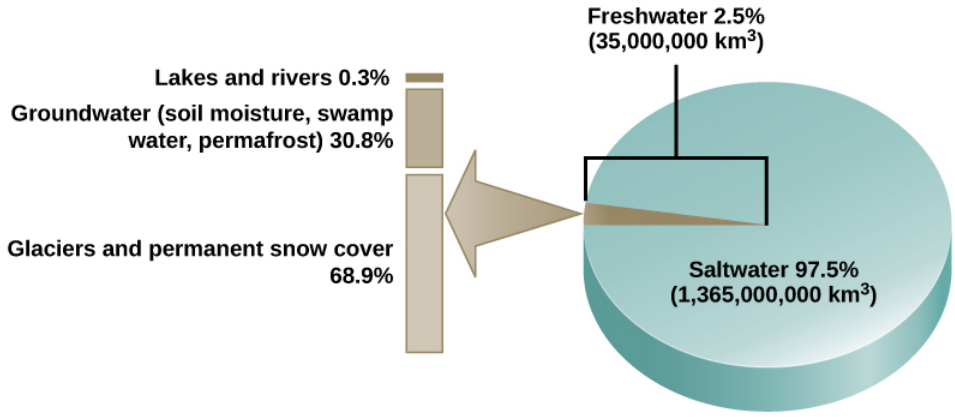


Figure 20.2.1: Only 2.5 percent of water on Earth is fresh water, and less than 1 percent of fresh water is easily accessible to living things.

Water cycling is extremely important to ecosystem dynamics. Water has a major influence on climate and, thus, on the environments of ecosystems, some located on distant parts of the Earth. Most of the water on Earth is stored for long periods in the oceans, underground, and as ice. Figure 20.2.2 illustrates the average time that an individual water molecule may spend in the Earth's major water reservoirs. **Residence time** is a measure of the average time an individual molecule stays in a particular reservoir. A large amount of the Earth's water is locked in place in these reservoirs as ice, beneath the ground, and in the ocean, and, thus, is unavailable for short-term cycling (only surface water can evaporate).

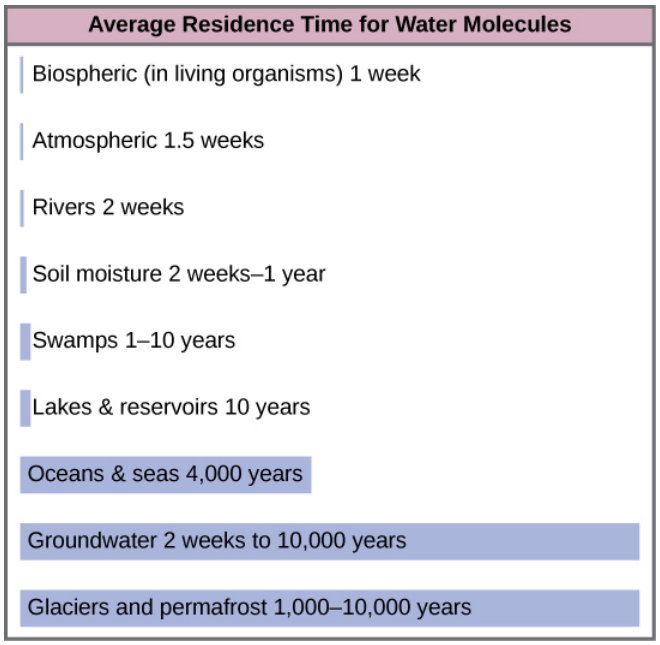


Figure 20.2.2: This graph shows the average residence time for water molecules in the Earth's water reservoirs.

There are various processes that occur during the cycling of water, shown in Figure 20.2.3. These processes include the following:

- evaporation/sublimation
- condensation/precipitation
- subsurface water flow
- surface runoff/snowmelt
- streamflow

The water cycle is driven by the sun's energy as it warms the oceans and other surface waters. This leads to the **evaporation** (water to water vapor) of liquid surface water and the **sublimation** (ice to water vapor) of frozen water, which deposits large amounts of water vapor into the atmosphere. Over time, this water vapor condenses into clouds as liquid or frozen droplets and is eventually followed by **precipitation** (rain or snow), which returns water to the Earth's surface. Rain eventually **infiltrates** into the ground,

where it may evaporate again if it is near the surface, flow beneath the surface, or be stored for long periods. More easily observed is surface **runoff**: the flow of fresh water either from rain or melting ice. Runoff can then make its way through streams and lakes to the oceans or flow directly to the oceans themselves.

Rain and surface runoff are major ways in which minerals, including carbon, nitrogen, phosphorus, and sulfur, are cycled from land to water. The environmental effects of runoff will be discussed later as these cycles are described.

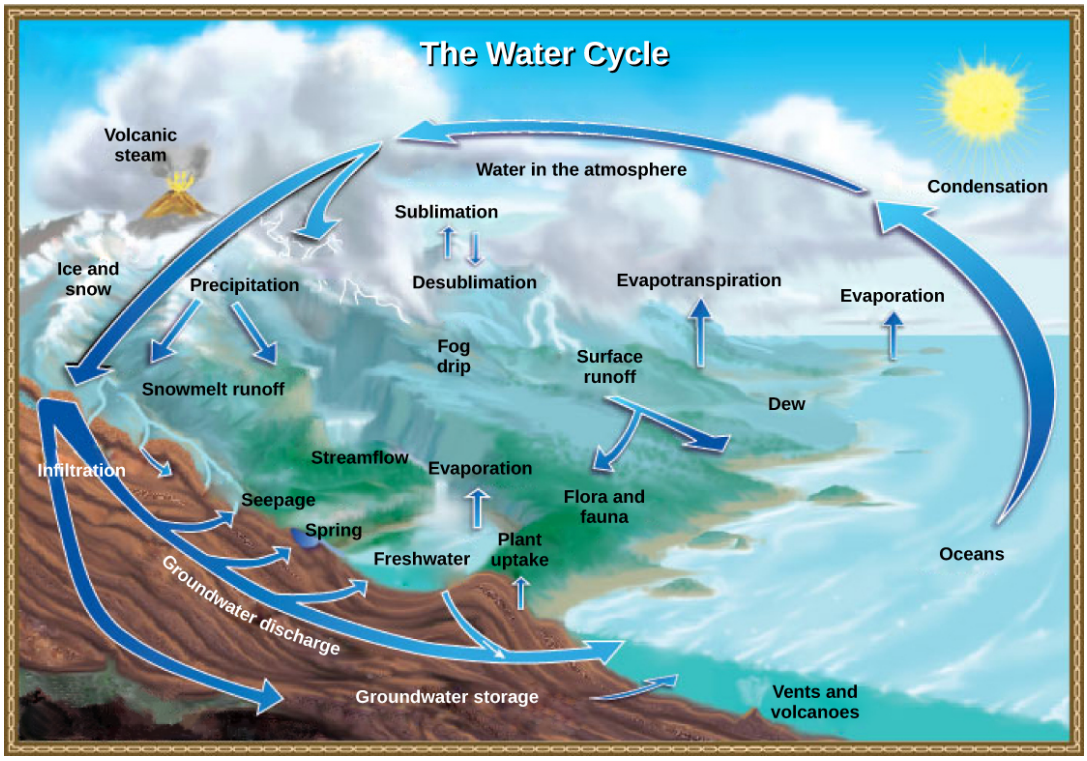


Figure 20.2.3: Water from the land and oceans enters the atmosphere by evaporation or sublimation, where it condenses into clouds and falls as rain or snow. Precipitated water may enter freshwater bodies or infiltrate the soil. The cycle is complete when surface or groundwater reenters the ocean. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

The Carbon Cycle

Carbon is the second most abundant element in living organisms. Carbon is present in all organic molecules, and its role in the structure of macromolecules is of primary importance to living organisms. Carbon compounds contain especially high energy, particularly those derived from fossilized organisms, mainly plants, which humans use as fuel. Since the 1800s, the number of countries using massive amounts of fossil fuels has increased. Since the beginning of the Industrial Revolution, global demand for the Earth's limited fossil fuel supplies has risen; therefore, the amount of carbon dioxide in our atmosphere has increased. This increase in carbon dioxide has been associated with climate change and other disturbances of the Earth's ecosystems and is a major environmental concern worldwide. Thus, a **carbon footprint** is based on how much carbon dioxide is produced and how much fossil fuel countries consume.

The carbon cycle is most easily studied as two interconnected sub-cycles: one dealing with rapid carbon exchange among living organisms and the other dealing with the long-term cycling of carbon through geologic processes. The entire carbon cycle is shown in Figure 20.2.4.

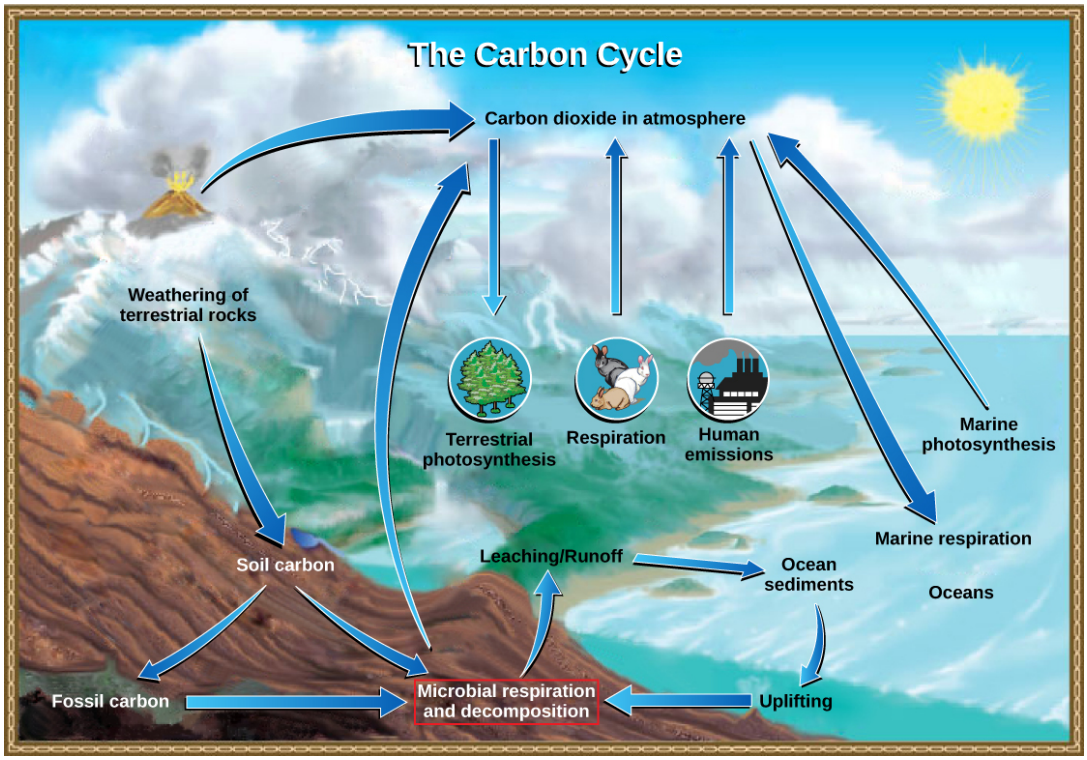


Figure 20.2.4: Carbon dioxide gas exists in the atmosphere and is dissolved in water. Photosynthesis converts carbon dioxide gas to organic carbon, and respiration cycles the organic carbon back into carbon dioxide gas. Long-term storage of organic carbon occurs when matter from living organisms is buried deep underground and becomes fossilized. Volcanic activity and, more recently, human emissions, bring this stored carbon back into the carbon cycle. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

The Biological Carbon Cycle

Living organisms are connected in many ways, even between ecosystems. A good example of this connection is the exchange of carbon between autotrophs and heterotrophs within and between ecosystems by way of atmospheric carbon dioxide. Carbon dioxide is the basic building block that most autotrophs use to build multi-carbon, high-energy compounds, such as glucose. The energy harnessed from the sun is used by these organisms to form the covalent bonds that link carbon atoms together. These chemical bonds thereby store this energy for later use in the process of respiration. Most terrestrial autotrophs obtain their carbon dioxide directly from the atmosphere, while marine autotrophs acquire it in the dissolved form (carbonic acid, $H_2CO_3^-$). However carbon dioxide is acquired, a by-product of the process is oxygen. The photosynthetic organisms are responsible for depositing approximately 21 percent oxygen content of the atmosphere that we observe today.

Heterotrophs and autotrophs are partners in biological carbon exchange (especially the primary consumers, largely herbivores). Heterotrophs acquire the high-energy carbon compounds from the autotrophs by consuming them and breaking them down by respiration to obtain cellular energy, such as ATP. The most efficient type of respiration, aerobic respiration, requires oxygen obtained from the atmosphere or dissolved in water. Thus, there is a constant exchange of oxygen and carbon dioxide between the autotrophs (which need the carbon) and the heterotrophs (which need the oxygen). Gas exchange through the atmosphere and water is one way that the carbon cycle connects all living organisms on Earth.

The Biogeochemical Carbon Cycle

The movement of carbon through the land, water, and air is complex, and in many cases, it occurs much more slowly geologically than as seen between living organisms. Carbon is stored for long periods in what are known as carbon **reservoirs**, which include the atmosphere, bodies of liquid water (mostly oceans), ocean sediment, soil, land sediments (including fossil fuels), and the Earth's interior.

As stated, the atmosphere is a major reservoir of carbon in the form of carbon dioxide and is essential to the process of photosynthesis. The level of carbon dioxide in the atmosphere is greatly influenced by the reservoir of carbon in the oceans. The

exchange of carbon between the atmosphere and water reservoirs influences how much carbon is found in each location, and each one affects the other reciprocally. Carbon dioxide (CO_2) from the atmosphere dissolves in water and combines with water molecules to form carbonic acid, and then it ionizes to carbonate and bicarbonate ions.

More than 90 percent of the carbon in the ocean is found as bicarbonate ions. Some of these ions combine with seawater calcium to form calcium carbonate ($CaCO_3$), a major component of marine organism shells. These organisms eventually form sediments on the ocean floor. Over geologic time, the calcium carbonate forms limestone, which comprises the largest carbon reservoir on Earth.

On land, carbon is stored in soil as a result of the decomposition of living organisms (by decomposers) or from weathering of terrestrial rock and minerals. This carbon can be leached into the water reservoirs by surface runoff. Deeper underground, on land and at sea, are fossil fuels: the anaerobically decomposed remains of plants that take millions of years to form. Fossil fuels are considered a **non-renewable resource** because their use far exceeds their rate of formation. A non-renewable resource, such as fossil fuel, is either regenerated very slowly or not at all. Another way for carbon to enter the atmosphere is from land (including land beneath the surface of the ocean) by the eruption of volcanoes and other geothermal systems. Carbon sediments from the ocean floor are taken deep within the Earth by the process of subduction: the movement of one tectonic plate beneath another. Carbon is released as carbon dioxide when a volcano erupts or from volcanic hydrothermal vents.

Carbon dioxide is also added to the atmosphere by the animal husbandry practices of humans. The large numbers of land animals raised to feed the Earth's growing population results in increased carbon dioxide levels in the atmosphere due to farming practices and animal respiration and methane production. This is another example of how human activity indirectly affects biogeochemical cycles in a significant way. Although much of the debate about the future effects of increasing atmospheric carbon on climate change focuses on fossils fuels, scientists take natural processes, such as volcanoes and respiration, into account as they model and predict the future impact of this increase.

? Optional Activity 20.2.1

Carbon is present in the atmosphere as

a. carbon dioxide
b. carbonate ion
c. carbon dust
d. carbon monoxide

Answer

a. carbon dioxide

The Nitrogen Cycle

Getting nitrogen into the living world is difficult. Plants and phytoplankton are not equipped to incorporate nitrogen from the atmosphere due to its chemistry, even though this molecule comprises approximately 78 percent of the atmosphere. Nitrogen enters the living world via free-living and symbiotic bacteria, which incorporate nitrogen into their macromolecules through **nitrogen fixation** (conversion of N_2). Cyanobacteria live in most aquatic ecosystems where sunlight is present; they play a key role in nitrogen fixation. Cyanobacteria are able to use inorganic sources of nitrogen to "fix" nitrogen. *Rhizobium* bacteria live symbiotically in the root nodules of legumes (such as peas, beans, and peanuts) and provide them with the organic nitrogen they need. Free-living bacteria, such as *Azotobacter*, are also important nitrogen fixers.

Organic nitrogen is especially important to the study of ecosystem dynamics since many ecosystem processes, such as primary production and decomposition, are limited by the available supply of nitrogen. As shown in Figure 20.2.5, the nitrogen that enters living systems by nitrogen fixation is successively converted from organic nitrogen back into nitrogen gas by bacteria. This process occurs in three steps in terrestrial systems: ammonification, nitrification, and denitrification. First, the **ammonification** process converts nitrogenous waste from living animals or from the remains of dead animals into ammonium (NH_4^+) by certain bacteria and fungi. Second, the ammonium is converted to nitrites (NO_2^-) by nitrifying bacteria, such as *Nitrosomonas*, through **nitrification**. Subsequently, nitrites are converted to nitrates (NO_3^-) by similar organisms. Third, the process of **denitrification**

occurs, whereby bacteria, such as *Pseudomonas* and *Clostridium*, convert the nitrates into nitrogen gas, allowing it to re-enter the atmosphere.

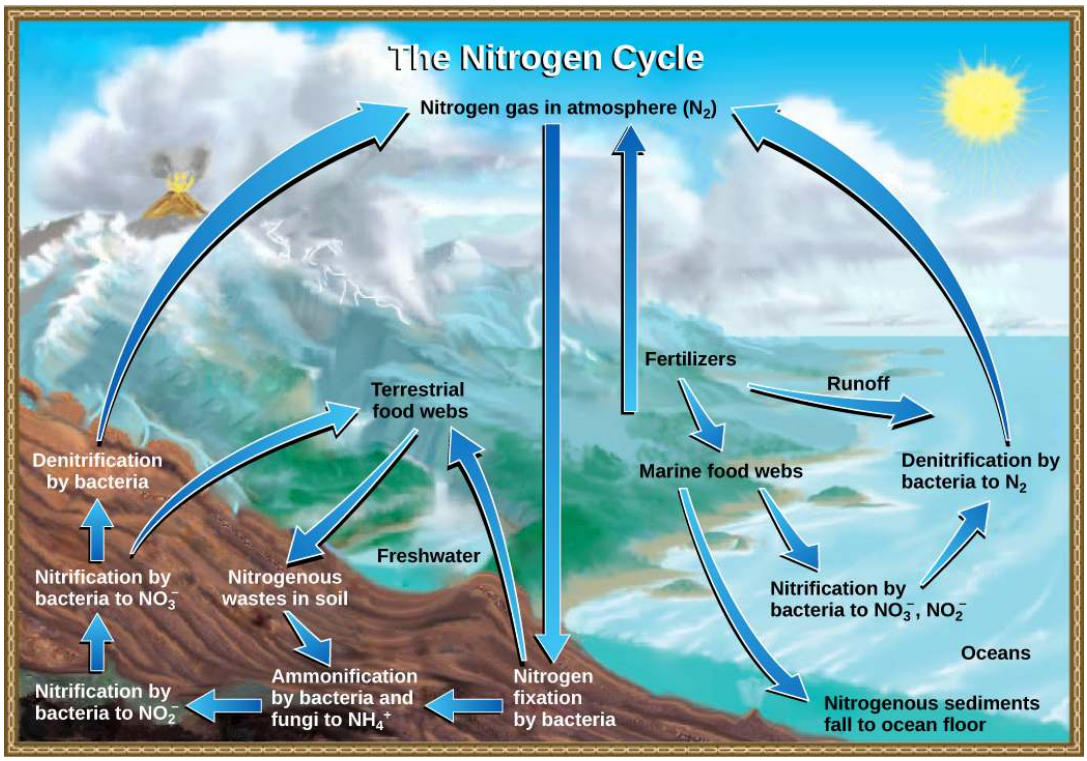


Figure 20.2.5: Nitrogen enters the living world from the atmosphere via nitrogen-fixing bacteria. This nitrogen and nitrogenous waste from animals is then processed back into gaseous nitrogen by soil bacteria, which also supply terrestrial food webs with the organic nitrogen they need. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

? Optional Activity 20.2.2

Which of the following statements about the nitrogen cycle is false?

A. Ammonification converts organic nitrogenous matter from living organisms into ammonium (NH_4^+).
B. Denitrification by bacteria converts nitrates (NO_3^-) to nitrogen gas (N_2).
C. Nitrification by bacteria converts nitrates (NO_3^-) to nitrites (NO_2^-).
D. Nitrogen fixing bacteria convert nitrogen gas (N_2) into organic compounds.

Answer

C. Nitrification by bacteria converts nitrates (NO_3^-) to nitrites (NO_2^-).

Human activity can release nitrogen into the environment by two primary means: the combustion of fossil fuels, which releases different nitrogen oxides, and by the use of artificial fertilizers in agriculture, which are then washed into lakes, streams, and rivers by surface runoff. Atmospheric nitrogen is associated with several effects on Earth's ecosystems including the production of acid rain (as nitric acid, HNO_3) and greenhouse gas (as nitrous oxide, N_2O) potentially causing climate change. A major effect from fertilizer runoff is saltwater and freshwater **eutrophication**, a process whereby nutrient runoff causes the excess growth of microorganisms, depleting dissolved oxygen levels and killing ecosystem fauna.

A similar process occurs in the marine nitrogen cycle, where the ammonification, nitrification, and denitrification processes are performed by marine bacteria. Some of this nitrogen falls to the ocean floor as sediment, which can then be moved to land in geologic time by uplift of the Earth's surface and thereby incorporated into terrestrial rock. Although the movement of nitrogen from rock directly into living systems has been traditionally seen as insignificant compared with nitrogen fixed from the

atmosphere, a recent study showed that this process may indeed be significant and should be included in any study of the global nitrogen cycle.[1]

The Phosphorus Cycle

Phosphorus is an essential nutrient for living processes; it is a major component of nucleic acid and phospholipids, and, as calcium phosphate, makes up the supportive components of our bones. Phosphorus is often the limiting nutrient (necessary for growth) in aquatic ecosystems (Figure 20.2.6).

Phosphorus occurs in nature as the phosphate ion (PO_4^{3-}). In addition to phosphate runoff as a result of human activity, natural surface runoff occurs when it is **leached** from phosphate-containing rock by weathering, thus sending phosphates into rivers, lakes, and the ocean. This rock has its origins in the ocean. Phosphate-containing ocean sediments form primarily from the bodies of ocean organisms and from their excretions. However, in remote regions, volcanic ash, aerosols, and mineral dust may also be significant phosphate sources. This sediment then is moved to land over geologic time by the uplifting of areas of the Earth's surface.

Phosphorus is also reciprocally exchanged between phosphate dissolved in the ocean and marine ecosystems. The movement of phosphate from the ocean to the land and through the soil is extremely slow, with the average phosphate ion having an oceanic residence time between 20,000 and 100,000 years.

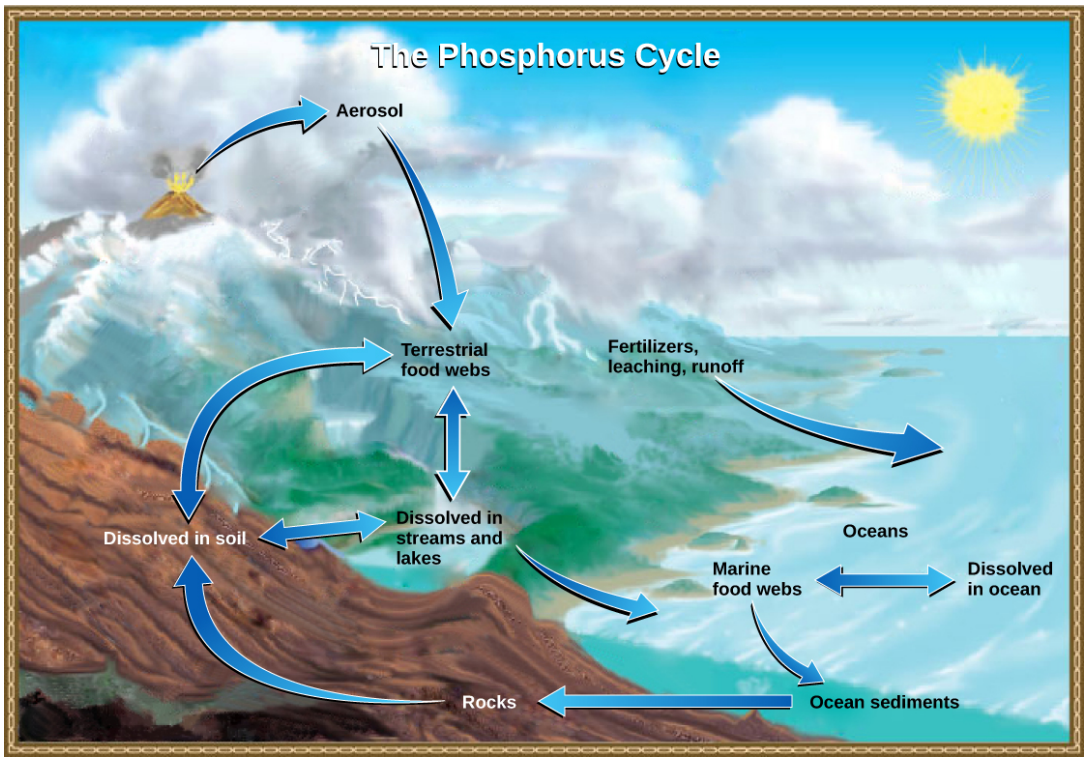


Figure 20.2.6: In nature, phosphorus exists as the phosphate ion (PO_4^{3-}). Weathering of rocks and volcanic activity releases phosphate into the soil, water, and air, where it becomes available to terrestrial food webs. Phosphate enters the oceans via surface runoff, groundwater flow, and river flow. Phosphate dissolved in ocean water cycles into marine food webs. Some phosphate from the marine food webs falls to the ocean floor, where it forms sediment. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

Excess phosphorus and nitrogen that enters these ecosystems from fertilizer runoff and from sewage causes excessive growth of microorganisms and depletes the dissolved oxygen, which leads to the death of many ecosystem fauna, such as shellfish and finfish. This process is responsible for dead zones in lakes and at the mouths of many major rivers (Figure 20.2.7).

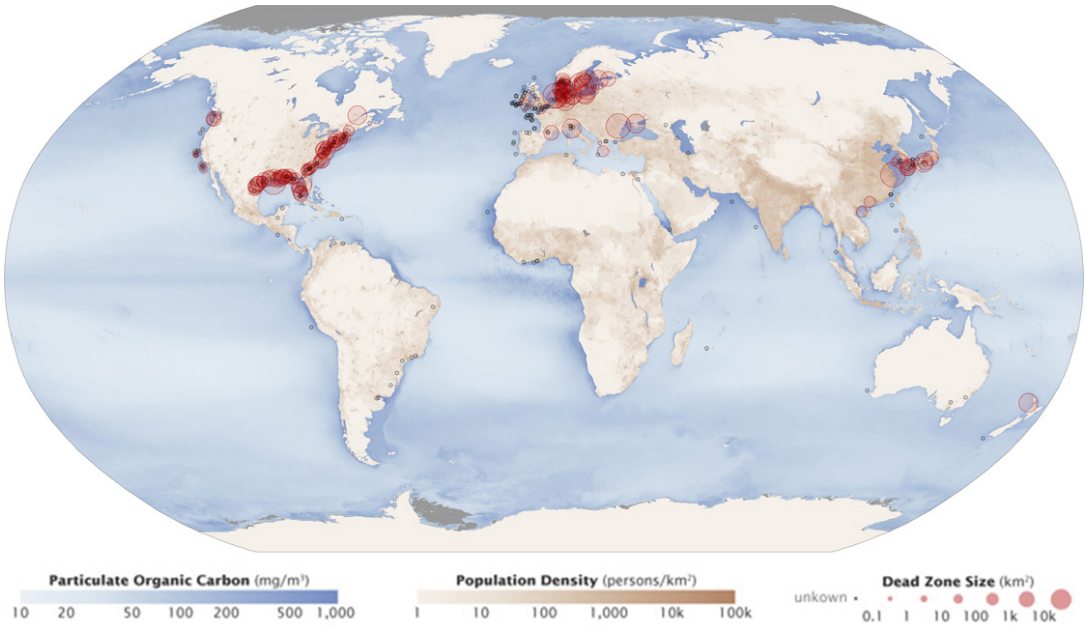


Figure 20.2.7: Dead zones occur when phosphorus and nitrogen from fertilizers cause excessive growth of microorganisms, which depletes oxygen and kills fauna. Worldwide, large dead zones are found in coastal areas of high population density. (credit: NASA Earth Observatory)

A **dead zone** is an area within a freshwater or marine ecosystem where large areas are depleted of their normal flora and fauna; these zones can be caused by eutrophication, oil spills, dumping of toxic chemicals, and other human activities. The number of dead zones has been increasing for several years, and more than 400 of these zones were present as of 2008. One of the worst dead zones is off the coast of the United States in the Gulf of Mexico, where fertilizer runoff from the Mississippi River basin has created a dead zone of over 8463 square miles. Phosphate and nitrate runoff from fertilizers also negatively affect several lake and bay ecosystems including the Chesapeake Bay in the eastern United States (Figure 20.2.8).

Everyday Connection: Chesapeake Bay

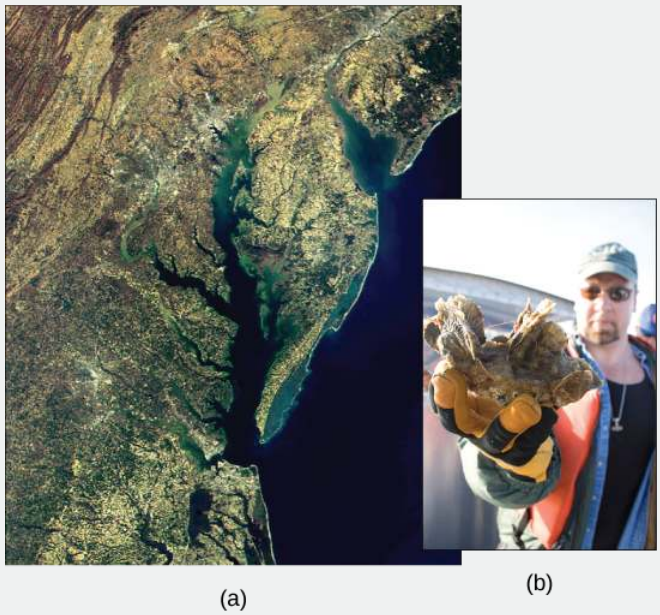


Figure 20.2.8: This (a) satellite image shows the Chesapeake Bay, an ecosystem affected by phosphate and nitrate runoff. A (b) member of the Army Corps of Engineers holds a clump of oysters being used as a part of the oyster restoration effort in the bay. (credit a: modification of work by NASA/MODIS; credit b: modification of work by U.S. Army)

The Chesapeake Bay has long been valued as one of the most scenic areas in the United States; it is now in distress and is recognized as a declining ecosystem. In the 1970s, the Chesapeake Bay was one of the first ecosystems to have identified dead

zones, which continue to kill many fish and bottom-dwelling species, such as clams, oysters, and worms. Several species have declined in the Chesapeake Bay due to surface water runoff containing excess nutrients from artificial fertilizer used on land. The source of the fertilizers (with high nitrogen and phosphate content) is not limited to agricultural practices. There are many nearby urban areas and more than 150 rivers and streams empty into the bay that are carrying fertilizer runoff from lawns and gardens. Thus, the decline of the Chesapeake Bay is a complex issue and requires the cooperation of industry, agriculture, and everyday homeowners.

Of particular interest to conservationists is the oyster population; it is estimated that more than 200,000 acres of oyster reefs existed in the bay in the 1700s, but that number has now declined to only 36,000 acres. Oyster harvesting was once a major industry for Chesapeake Bay, but it declined 88 percent between 1982 and 2007. This decline was due not only to fertilizer runoff and dead zones but also to overharvesting. Oysters require a certain minimum population density because they must be in close proximity to reproduce. Human activity has altered the oyster population and locations, greatly disrupting the ecosystem.

The restoration of the oyster population in the Chesapeake Bay has been ongoing for several years with mixed success. Not only do many people find oysters good to eat, but they also clean up the bay. Oysters are filter feeders, and as they eat, they clean the water around them. In the 1700s, it was estimated that it took only a few days for the oyster population to filter the entire volume of the bay. Today, with changed water conditions, it is estimated that the present population would take nearly a year to do the same job.

Restoration efforts have been ongoing for several years by non-profit organizations, such as the Chesapeake Bay Foundation. The restoration goal is to find a way to increase population density so the oysters can reproduce more efficiently. Many disease-resistant varieties (developed at the Virginia Institute of Marine Science for the College of William and Mary) are now available and have been used in the construction of experimental oyster reefs. Efforts to clean and restore the bay by Virginia and Delaware have been hampered because much of the pollution entering the bay comes from other states, which stresses the need for inter-state cooperation to gain successful restoration.

The new, hearty oyster strains have also spawned a new and economically viable industry—oyster aquaculture—which not only supplies oysters for food and profit, but also has the added benefit of cleaning the bay.

Learn about the ecology of *natural* dead zones in the Saanich Inlet in British Columbia here: https://www.uvic.ca/science/home/news/archive/saanich%20inlet%20project.php

The Sulfur Cycle

Sulfur is an essential element for the macromolecules of living things. As a part of the amino acid cysteine, it is involved in the formation of disulfide bonds within proteins, which help to determine their 3-D folding patterns, and hence their functions. As shown in Figure 20.2.9, sulfur cycles between the oceans, land, and atmosphere. Atmospheric sulfur is found in the form of sulfur dioxide (SO_2) and enters the atmosphere in three ways: from the decomposition of organic molecules, from volcanic activity and geothermal vents, and from the burning of fossil fuels by humans.

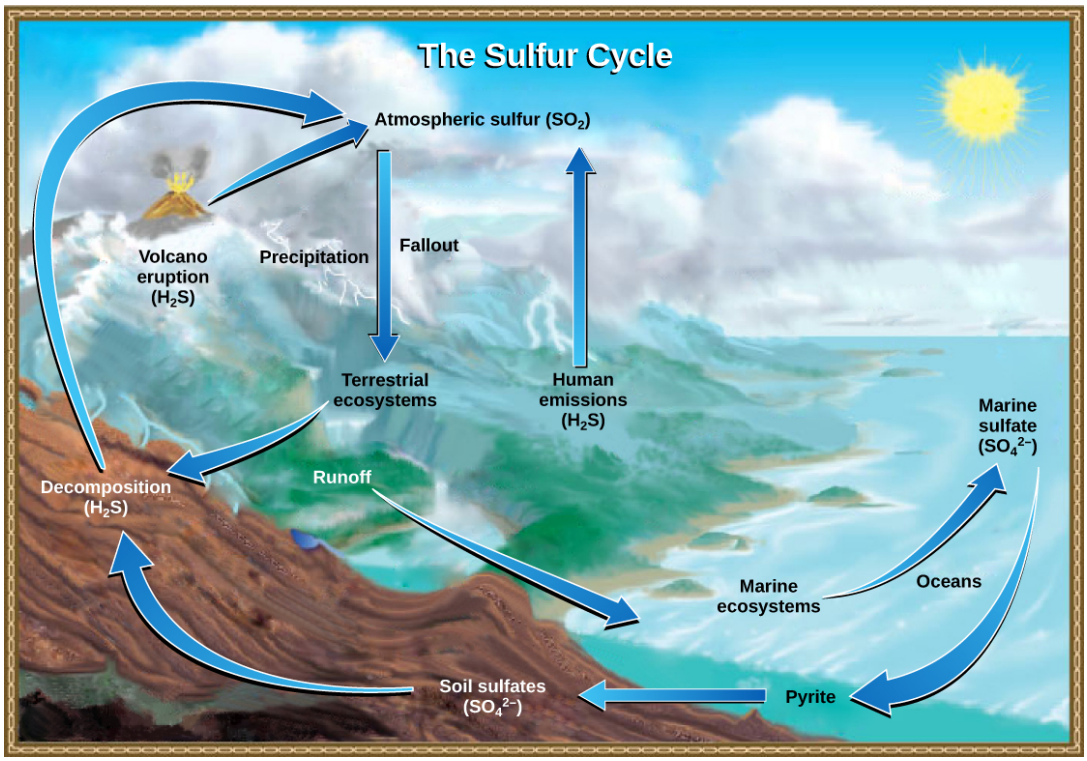


Figure 20.2.9: Sulfur dioxide from the atmosphere becomes available to terrestrial and marine ecosystems when it is dissolved in precipitation as weak sulfuric acid or when it falls directly to the Earth as fallout. Weathering of rocks also makes sulfates available to terrestrial ecosystems. Decomposition of living organisms returns sulfates to the ocean, soil and atmosphere. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

On land, sulfur is deposited in four major ways: precipitation, direct fallout from the atmosphere, rock weathering, and geothermal vents (Figure 20.2.10). Atmospheric sulfur is found in the form of sulfur dioxide (SO_2), and as rain falls through the atmosphere, sulfur is dissolved in the form of weak sulfuric acid (H_2SO_4). Sulfur can also fall directly from the atmosphere in a process called fallout.

Also, the weathering of sulfur-containing rocks releases sulfur into the soil. These rocks originate from ocean sediments that are moved to land by the geologic uplifting of ocean sediments. Terrestrial ecosystems can then make use of these soil sulfates (SO_4^{2-}), and upon the death and decomposition of these organisms, release the sulfur back into the atmosphere as hydrogen sulfide (H_2S) gas. Sulfur enters the ocean via runoff from land, from atmospheric fallout, and from underwater geothermal vents. Some ecosystems rely on chemoautotrophs using sulfur as a biological energy source. This sulfur then supports marine ecosystems in the form of sulfates.



Figure 20.2.10: At this sulfur vent in Lassen Volcanic National Park in northeastern California, the yellowish sulfur deposits are visible near the mouth of the vent.

Human activities have played a major role in altering the balance of the global sulfur cycle. The burning of large quantities of fossil fuels, especially coal, releases larger amounts of hydrogen sulfide gas into the atmosphere. As rain falls through this gas, it creates the phenomenon known as acid rain. **Acid rain** is corrosive rain caused by rainwater falling to the ground through sulfur dioxide gas, turning it into weak sulfuric acid, which causes damage to aquatic ecosystems. Acid rain damages the natural environment by lowering the pH of lakes, which kills many of the resident fauna; it also affects the man-made environment through the chemical degradation of buildings. For example, many marble monuments, such as the Lincoln Memorial in Washington, DC, have suffered significant damage from acid rain over the years. These examples show the wide-ranging effects of human activities on our environment and the challenges that remain for our future.

? Optional Activity 20.2.3

The average time a molecule spends in its reservoir is known as _____.

a. residence time
b. restriction time
c. resilience time
d. storage time

Answer

a. residence time

? Optional Activity 20.2.4

The process whereby nitrogen is brought into organic molecules is called _____.

a. ammonification
b. denitrification
c. nitrogen fixation
d. nitrogen cycling

Answer

c. nitrogen fixation

Footnotes

1. 1 Scott L. Morford, Benjamin Z. Houlton, and Randy A. Dahlgren, “Increased Forest Ecosystem Carbon and Nitrogen Storage from Nitrogen Rich Bedrock,” *Nature* 477, no. 7362 (2011): 78–81.

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20.3: Eutrophication and Dead Zones

Key Points

- Excess phosphorus and nitrogen in the ecosystem leads to the death of many organisms, causing dead zones.
- Dead zones are caused by by eutrophication, oil spills, dumping of toxic chemicals, and other human activities.

Key Terms

- **eutrophication**: process whereby excess levels of nitrogen or phosphorus cause excessive growth of microorganisms, depleting dissolved oxygen levels and kill ecosystem fauna
- **dead zone**: an area within a freshwater or marine ecosystem where large areas are depleted of their normal flora and fauna; caused by excessive nutrient pollution

Eutrophication and Dead Zones

Nutrients in soil and water are generally beneficial when they exist at naturally occurring levels. Nitrogen fertilizers have been applied to farm fields for decades in order to maximize production of agricultural lands. However, an unintended consequence is that the same nutrients can be detrimental to aquatic ecosystems when introduced excessively for agricultural or other purposes. Nitrogen (N) and Phosphorus (P) are introduced by fertilizers that are used intensively in agriculture, as well as golf courses and some lawns and gardens. Farm animal waste and sewage also provide large amounts of reactive N and P. Phosphorus was formerly used heavily as an additive in laundry and dishwater detergents, but since the 1970's it has been phased out in both through a combination of state and federal regulations. Overall, our modern society has altered the global N and P cycles such that there is an overabundance in many settings.

Excessive nutrients (not utilized) are often washed into drainage ways, streams, and rivers during rainfall and storm events. **Eutrophication** occurs when excess phosphorus and nitrogen from fertilizer runoff or sewage causes excessive growth of algae. Algal blooms that block light and therefore kill aquatic plants in rivers, lakes, and seas. The subsequent death and decay of these organisms depletes dissolved oxygen, which leads to the death of aquatic organisms such as shellfish and fish. This process is responsible for **dead zones**, large areas in lakes and oceans near the mouths of rivers that are periodically depleted of their normal flora and fauna, and for massive fish kills, which often occur during the summer months (figure 20.3.1). There are more than 500 dead zones worldwide. Phosphate and nitrate runoff from fertilizers also negatively affect several lake and bay ecosystems including the Chesapeake Bay in the eastern United States.

One of the worst dead zones is off the coast of the United States in the Gulf of Mexico (figure 20.3.1). Fertilizer runoff from the Mississippi River basin created a dead zone, which reached its peak size of 8,776 square miles in 2017. The Mississippi River dumps high-nutrient runoff from its drainage basin that includes vast agricultural lands in the American Midwest. Increased algal growth produced by these nutrients has affected important shrimp fishing grounds in the Gulf. The primary source of the nutrients is the heavily tile-drained areas of farmland in the Midwest corn and soybean belt (SW Minnesota, N Iowa, NE Illinois, N Indiana and NW Ohio). Improved soil drainage systems over the past century or more have allowed for effective transport of nitrate compounds as stormwater runoff into drainage basins (Ohio River, Wabash River, Illinois River, Missouri River, etc.) that feed into the Mississippi River. Prior to drainage, these wetlands would also have removed nutrients through denitrification and other biogeochemical processes. In other words, the same drainage tiles that allow for the agricultural benefit of having rich bottomland/wetland soils in production, have the disadvantage of increased and more rapid movements of nitrate solutes to the Gulf of Mexico. Such large-scale problems, across state governmental boundaries, can only be fully addressed in the future with a national system of incentives, regulations, or laws.

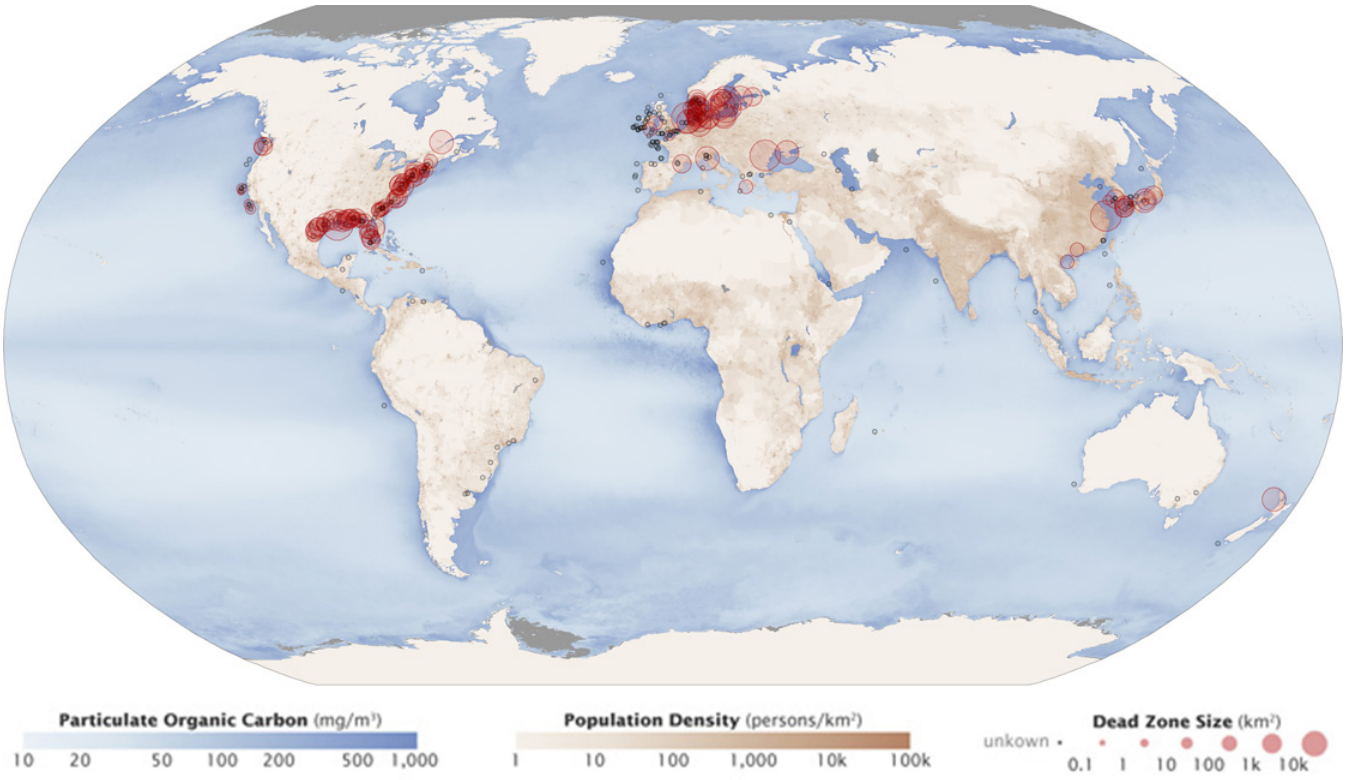


Figure 20.3.1**:** Dead zones occur when phosphorus and nitrogen from fertilizers cause excessive growth of microorganisms, which depletes oxygen and kills fauna. This map shows dead zones around the world in 2008. Worldwide, large dead zones are found in coastal areas of high population density (credit: NASA Earth Observatory).

In addition to fertilizers, nitrogen inputs to watersheds can also include atmospheric deposition, livestock waste, and sewage, but nitrogen fertilizers comprise a significant majority of the input to monitored streams, particularly in springtime when much fertilizer is applied. Possible solutions to this problem include encouraging farmers to apply a more limited quantity of fertilizer in the spring (only as much as necessary), rather than in the fall, to allow for considerably less time for stormwater or meltwater runoff. Other solutions include maintaining cover crops, or restoring wetlands in key locations to contain nitrate losses. An overall strategy that limits the excess capacity of nutrients can simultaneously benefit farmers (by limiting cost), the ecology of stream watersheds and coastal ecosystems (also locally stressed by oil spills and other pollution). Over the long term, more efforts will need to be made in the Mississippi River Basin, and globally in similarly stressed agricultural or urban watersheds (figure 20.3.1), to improve the health and sustainability of our soil, land, and aquatic ecosystems.

Everyday Connection: Chesapeake Bay

The Chesapeake Bay has long been valued as one of the most scenic areas on Earth; it is now in distress and is recognized as a declining ecosystem. In the 1970s, the Chesapeake Bay was one of the first ecosystems to have identified dead zones, which continue to kill many fish and bottom-dwelling species, such as clams, oysters, and worms (Figure 20.3.2). Several species have declined in the Chesapeake Bay due to surface water runoff containing excess nutrients from artificial fertilizer used on land. The source of the fertilizers (with high nitrogen and phosphate content) is not limited to agricultural practices. There are many nearby urban areas and more than 150 rivers and streams empty into the bay that are carrying fertilizer runoff from lawns and gardens. Thus, the decline of the Chesapeake Bay is a complex issue and requires the cooperation of industry, agriculture, and everyday homeowners.



(a) (b)

Figure 20.3.2**:** This (a) satellite image shows the Chesapeake Bay, an ecosystem affected by phosphate and nitrate runoff. A (b) member of the Army Corps of Engineers holds a clump of oysters being used as a part of the oyster restoration effort in the bay (credit a: modification of work by NASA/MODIS; credit b: modification of work by U.S. Army).

Of particular interest to conservationists is the oyster population; it is estimated that more than 200,000 acres of oyster reefs existed in the bay in the 1700s, but that number has now declined to only 36,000 acres. Oyster harvesting was once a major industry for Chesapeake Bay, but it declined 88 percent between 1982 and 2007. This decline was due not only to fertilizer runoff and dead zones but also to overexploitation. Oysters require a certain minimum population density because they must be in close proximity to reproduce. Human activity has altered the oyster population and locations, greatly disrupting the ecosystem.

The restoration of the oyster population in the Chesapeake Bay has been ongoing for several years with mixed success. Not only do many people find oysters good to eat, but they also clean up the bay. Oysters are filter feeders, and as they eat, they clean the water around them. In the 1700s, it was estimated that it took only a few days for the oyster population to filter the entire volume of the bay. Today, with changed water conditions, it is estimated that the present population would take nearly a year to do the same job.

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The new, hearty oyster strains have also spawned a new and economically viable industry—oyster aquaculture—which not only supplies oysters for food and profit, but also has the added benefit of cleaning the bay.

Suggested Supplementary Reading

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CHAPTER OVERVIEW

Chapter 21: Landscape Ecology and Island Biogeography

Learning Objectives

- Understand the origins and aims of Landscape Ecology
- Learn some of the important terms used in Landscape Ecology
- Understand the basics of the Theory of Island Biogeography
- Make connections between the Theory of Island Biogeography and its application in Ecology

21.1: What is Landscape Ecology?
21.2: Applications of Landscape Ecology
21.3: Island Biogeography

Summary

Landscape ecology is the science of studying and improving relationships between ecological processes in the environment and particular ecosystems. This is done within a variety of landscape scales, development spatial patterns, and organizational levels of research and policy. Landscape ecology often focuses on the composition of landscapes, and how the size, shape, and adjacency of different habitat patches affect ecological processes. The development of the Theory of Island Biogeography in the 1960s was fundamental to our understanding of how the size and isolation of habitat patches affect the life histories of species found within them. This, in turn, resulted in a strong focusses on habitat fragmentation within the subfield of Landscape Ecology.

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21.1: What is Landscape Ecology?

Introduction

Landscape ecology is the study of the pattern and interaction between ecosystems within a region of interest, and the way the interactions affect ecological processes, especially the unique effects of spatial heterogeneity on these interactions. This is done within a variety of landscape scales, development spatial patterns, and organizational levels of research and policy. Concisely, landscape ecology can be described as the science of landscape diversity as the synergetic result of biodiversity and geodiversity.

As a highly interdisciplinary field in systems science, landscape ecology integrates biophysical and analytical approaches with humanistic and holistic perspectives across the natural sciences and social sciences. Landscapes are spatially heterogeneous geographic areas characterized by diverse interacting patches or ecosystems, ranging from relatively natural terrestrial and aquatic systems such as forests, grasslands, and lakes to human-dominated environments including agricultural and urban settings.

The most salient characteristics of landscape ecology are its emphasis on the relationship among pattern, process, and scale, and its focus on broad-scale ecological and environmental issues. These necessitate the coupling between biophysical and socioeconomic sciences. Key research topics in landscape ecology include ecological flows in landscape mosaics, land use and land cover change, scaling, relating landscape pattern analysis with ecological processes, and landscape conservation and sustainability. Landscape ecology also studies the role of human impacts on landscape diversity in the development and spreading of new human pathogens that could trigger epidemics.

Heterogeneity is the measure of how parts of a landscape differ from one another. Landscape ecology looks at how this spatial structure affects organism abundance at the landscape level, as well as the behavior and functioning of the landscape as a whole. This includes studying the influence of pattern, or the internal order of a landscape, on process, or the continuous operation of functions of organisms. Landscape ecology also includes geomorphology as applied to the design and architecture of landscapes. Geomorphology is the study of how geological formations are responsible for the structure of a landscape.

Terminology and Concepts

Scale and Heterogeneity

Imaging and mapping technology naturally promoted a patch-corridor-matrix approach to landscape ecology (Figure 21.1.1). Examining the map of an area in North Dakota (Figure 21.1.2) helps to define important vocabulary and illustrates some typical questions studied by landscape ecologists. A patch is an area of habitat differing from its surroundings, often the smallest ecologically distinct landscape feature in a landscape mapping and classification system. In Figure 21.1.2, wetlands and perennial grasslands would likely be patches of focal interest for the study of ecological processes. The matrix is the majority of the surrounding landscape (i.e., not the patches); in this case the matrix primarily consists of fields of agricultural crops. The large proportion of the landscape classified as matrix may have profound influences on the ecological processes in the landscape; for example, consider the flow of pesticides from the farmed matrix to the wetland patches in Figure 21.1.2. Finally, corridors are narrow patches that may act as links or barriers in a landscape. Beyond the image of narrow patches, corridors are functionally important landscape structures influencing dispersal of plants and animals in the landscape.

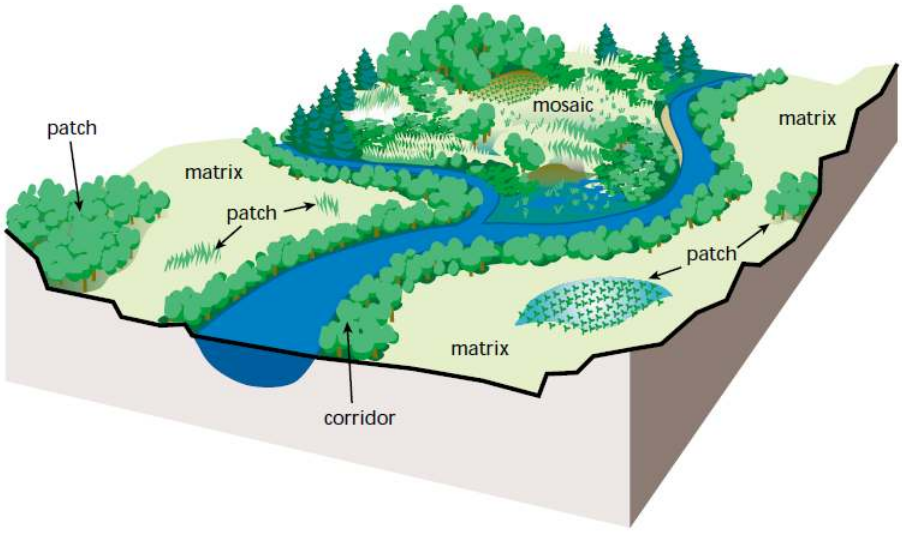


Figure 21.1.1: Basic terms to define landscape ecology (FISGRW 1998) from *Understanding Landscape Structure Using Landscape Metrics* (Ercan Gökyer) (DOI: 10.5772/55758)

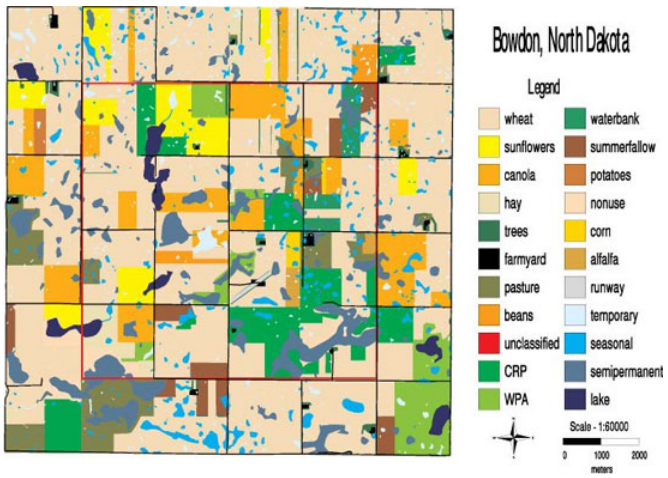


Figure 21.1.2: A map of classified habitats in the landscape near Bowdon, North Dakota, USA. Patches of interest include the wetlands (blue) and perennial grasslands (green) surrounded by a matrix of agricultural crops (primarily tan, yellow and orange). Note the gravel roads (black) spaced one mile apart. The red box encloses 16 mi^2.

Composition and Patches

Composition is the relative proportion of habitat types in the landscape, regardless of spatial distribution; for example, in Figure 21.1.2 perennial grasslands comprise 17%, wetlands about 18%, and croplands about 56% of the landscape. Configuration refers to almost limitless aspects of landscape heterogeneity, especially the physical and spatial distribution of landscape elements. Configuration metrics that apply across an entire landscape would include characteristics such as the dendritic pattern of streams in a watershed, or the diversity of habitat types. Ecologists have been particularly interested in how the spatial distribution of elements affects ecological processes. For example, “is the percentage of wetlands occupied by tiger salamanders (*Ambystoma tigrinum*) influenced by whether wetlands are distributed randomly or clumped to some degree?” (Figure 21.1.2). Another sense of configuration focuses on the characteristics of patches (e.g., the size, shape, or perimeter to area ratio [P/A] of individual patches). This latter emphasis is often prompted by interest in a particular organism that uses a patch type as habitat (e.g., grassland birds nesting in the landscape) (Figure 21.1.2). P/A is a measure of the amount of edge (or ecotone) between a focal patch type and the surrounding matrix. Ecotones represent transitional zones that often have important influences on ecological processes. In Figure 21.1.2, landscape ecologists have asked, “do predators search for nests in the same patterns along edges compared to interiors of grassland patches?”.

There are many other terms (see below) and metrics that are used to describe landscapes, but two others are particularly important to understand. In an ecological sense scale is the resolution at which an organism perceives its environment (e.g., consider a mouse population versus a moose population). Scale is important to plants too; “what is the detectable limit over which seeds disperse from a plant?” Often scale is also used in a technological sense referring to the smallest area that can be resolved into a single type on the landscape. Spatial scale of remotely sensed vegetation may be as small as 0.5 m, although for large areas it is more typically 30 m, or greater. Extent is the extended range of study, or the area included within the landscape boundary, such as a national park or state.

Boundary and edge

Landscape patches have a boundary between them which can be defined or fuzzy. The zone composed of the edges of adjacent ecosystems is the *boundary*. *Edge* means the portion of an ecosystem near its perimeter, where influences of the adjacent patches can cause an environmental difference between the interior of the patch and its edge. This edge effect includes a distinctive species composition or abundance. For example, when a landscape is a mosaic of perceptibly different types, such as a forest adjacent to a grassland, the edge is the location where the two types adjoin. In a continuous landscape, such as a forest giving way to open woodland, the exact edge location is fuzzy and is sometimes determined by a local gradient exceeding a threshold, such as the point where the tree cover falls below thirty-five percent.

Ecotones, ecoclines, and ecotopes

A type of boundary is the *ecotone*, or the transitional zone between two communities.Ecotones can arise naturally, such as a lakeshore, or can be human-created, such as a cleared agricultural field from a forest. The ecotonal community retains characteristics of each bordering community and often contains species not found in the adjacent communities. Classic examples of ecotones include fencerows, forest to marshlands transitions, forest to grassland transitions, or land-water interfaces such as riparian zones in forests. Characteristics of ecotones include vegetational sharpness, physiognomic change, occurrence of a spatial community mosaic, many exotic species, ecotonal species, spatial mass effect, and species richness higher or lower than either side of the ecotone.

An *ecocline* is another type of landscape boundary, but it is a gradual and continuous change in environmental conditions of an ecosystem or community. Ecoclines help explain the distribution and diversity of organisms within a landscape because certain organisms survive better under certain conditions, which change along the ecocline. They contain heterogeneous communities which are considered more environmentally stable than those of ecotones. An *ecotope* is a spatial term representing the smallest ecologically distinct unit in mapping and classification of landscapes. Relatively homogeneous, they are spatially explicit landscape units used to stratify landscapes into ecologically distinct features. They are useful for the measurement and mapping of landscape structure, function, and change over time, and to examine the effects of disturbance and fragmentation.



Figure 21.1.3: An ecotone between grassland and woodland (source: https://commons.wikimedia.org/wiki/F...967532722).jpg)

Disturbance and fragmentation

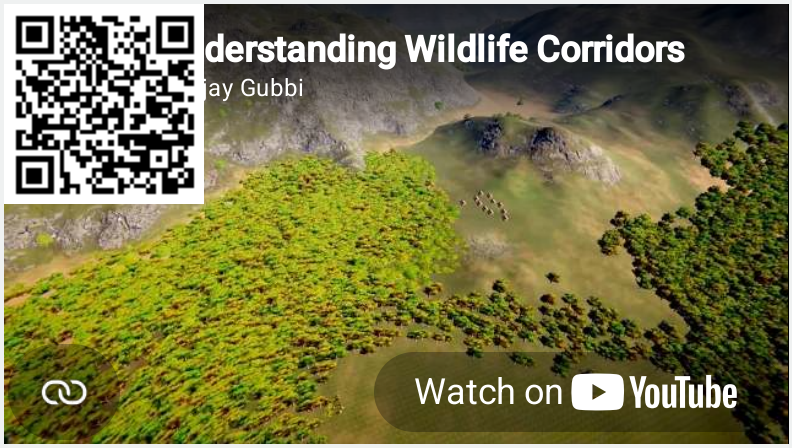
Disturbance is an event that significantly alters the pattern of variation in the structure or function of a system. *Fragmentation* is the breaking up of a habitat, ecosystem, or land-use type into smaller parcels.Disturbance is generally considered a natural process. Fragmentation causes land transformation, an important process in landscapes as development occurs.

An important consequence of repeated, random clearing (whether by natural disturbance or human activity) is that contiguous cover can break down into isolated patches. This happens when the area cleared exceeds a critical level, which means that landscapes exhibit two phases: connected and disconnected.



Figure 21.1.4: Rapid deforestation in Cambodia resulted in habitat loss and fragmentation (Global Forest Watch. World Resources Institute. Accessed on 1/5/2022. www.globalforestwatch.org)

Video



History

Throughout the history of ecology, scientists have observed variability across time and space in the abiotic and biotic components of ecosystems. But early ecologists did not have the technology or concepts to explicitly deal with spatial heterogeneity, so there was a tendency to develop explanations by grouping organisms into uniform and recognizable units. For example, scientists were struck by the relatively consistent associations of plant species and grouped vegetation into community types (Mueller-Dombois & Ellenberg 1974). Compared to vegetation, where observed change was rather slow, observations of fluctuating populations ranging from bacteria and protozoans in the laboratory to snowshoe hares (*Lepus americanus*) in the boreal forest, led scientists to mathematical theories that explicitly focused on temporal dynamics (Kingsland 1995). But the resulting models treated the environment as spatially homogeneous. Such views of nature and the theory about dynamics led to “equilibrium” concepts (May 1973) that dominated ecological thinking from the 1920s through the 1980s.

During the 1980s, advances in the accessibility of computing, remotely sensed satellite and aerial imagery, development of geographic information systems (GIS, ARC/INFO was first released in 1982), and spatial statistical methods (Fortin & Dale 2005), enabled ecologists to observe and analyze spatial heterogeneity ranging from local habitats to entire continents. The technology enhanced a paradigm shift occurring in ecology and the emergence of landscape ecology as a sub-discipline within ecology (Wu & Loucks 1995). Landscape ecology specifically recognizes that disturbance, whether anthropogenic or caused by natural processes, creates spatial heterogeneity that is the normal condition of ecosystems. In landscape ecology particularly, a “non-equilibrium” view emerged, that links disturbance in time and space to system structure and function in feedback loops that influence the ecology and evolutionary trajectories in the ecosystems. The International Association of Landscape Ecology was formed in 1982. In 1986, Forman and Godron published their seminal text on landscape ecology. This work was important, not only because it outlined principles, but also because it brought together the North American scientific interest — typically focused on heterogeneity in ecosystems — with more anthropocentric scientific traditions of geography, landscape architecture, and planning, rooted in the long history of landscape alteration in Europe.

One central landscape ecology theory originated from MacArthur & Wilson's The Theory of Island Biogeography (see 21.3). The concepts of island biogeography were generalized from physical islands to abstract patches of habitat. This generalization spurred the growth of landscape ecology by providing conservation biologists a new tool to assess how habitat fragmentation affects population viability. Recent growth of landscape ecology owes much to the development of geographic information systems (GIS) and the availability of large-extent habitat data (e.g. remotely sensed datasets) Figure 21.1.1.

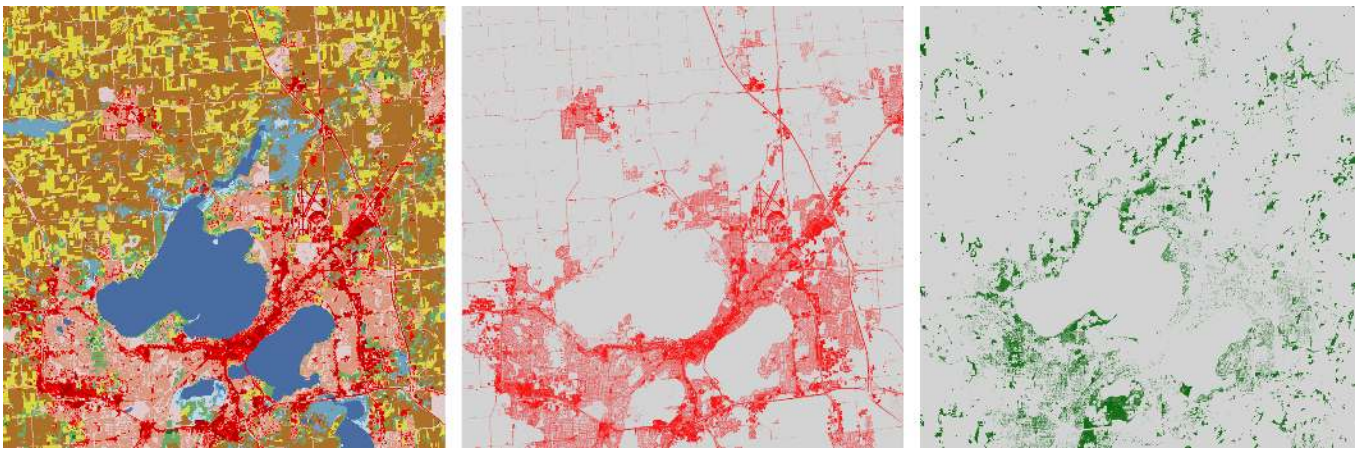


Figure 21.1.1: Land cover surrounding Madison, WI. Left: fields are colored yellow and brown, water is colored blue, and urban surfaces are colored red. Center: impervious surfaces. Right: canopy cover.

Development as a discipline

Today, the theory and application of landscape ecology continue to develop through a need for innovative applications in a changing landscape and environment. Landscape ecology relies on advanced technologies such as remote sensing, GIS, and models. There has been associated development of powerful quantitative methods to examine the interactions of patterns and processes. An example would be determining the amount of carbon present in the soil based on landform over a landscape, derived from GIS maps, vegetation types, and rainfall data for a region. Remote sensing work has been used to extend landscape ecology to the field of predictive vegetation mapping.

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21.2: Applications of Landscape Ecology

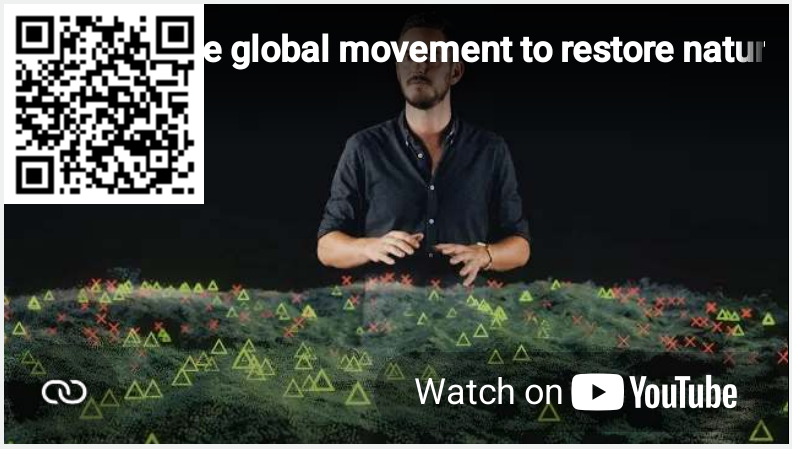
Themes of Study and Application

The development and dynamics of spatial heterogeneity in landscapes is a central theme of ecological studies, especially the effects of conversion of natural ecosystems into human-dominated systems such as agricultural or urban land use. As natural habitat is altered in a landscape (both the composition (forest area) and the configuration (spatial pattern of patches) change. This conversion is called fragmentation (Figure 21.2.1). Evidence is mounting that change in composition has a dominant effect on composition of the biota, whereas variation in configuration has a lesser effect, except at very low proportion of patch composition in the landscape. Such ideas have practical consequences for the conservation of biodiversity. Rhetorically, “will protection of a Single Large patch of habitat or Several Small patches (the SLOSS tradeoff) have equivalent effects on species persistence or biodiversity?"



Figure 21.2.1: Clearcut logging in forests of the Pacific Northwest, USA. Notice that some cut patches are relatively recent, with bare ground exposed, whereas vegetation has begun to reestablish itself in others.

Video



Another theme relating configuration and conservation is the potential value of corridors linking habitats. Across large parts of the globe, biodiversity is affected by the interactions between climate changes and landscape linkages, and land use, which may block (barriers) or enhance (corridors) species persistence. Although ecologists have debated the scientific evidence concerning the effect of corridors, like SLOSS, the idea of landscape linkages has intuitive appeal for conservation. For example, conservationists interested in large predators have used knowledge of their movements, coupled with habitat data in GIS analyses, to identify focal areas for conservation corridors (Figure 2). Conversely, when the motivating question is related to the spread of an invasive insect like emerald ash borer (*Agrilus planipennis*), or an emerging infectious disease like avian influenza, then corridors and patches that

act as stepping stones have negative rather than positive value. Recent combinations of population genetics and landscape ecology have strengthened the ability to understand how species respond to landscape change, because they have the potential to reveal patterns of dispersal linkages and barriers across extensive regions. Landscape genetics provides a conceptual framework and tools to link the ecological short-term and local spatial scale with the long-term and large spatial scale helpful in understanding adaptation.

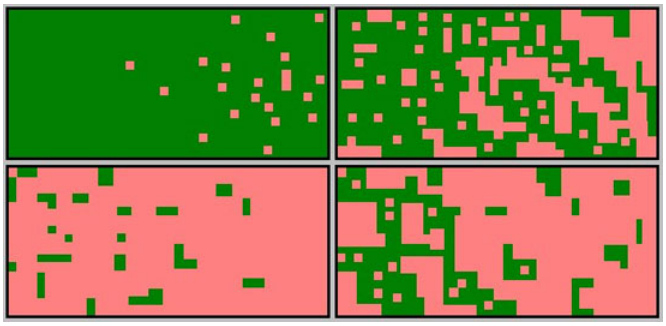
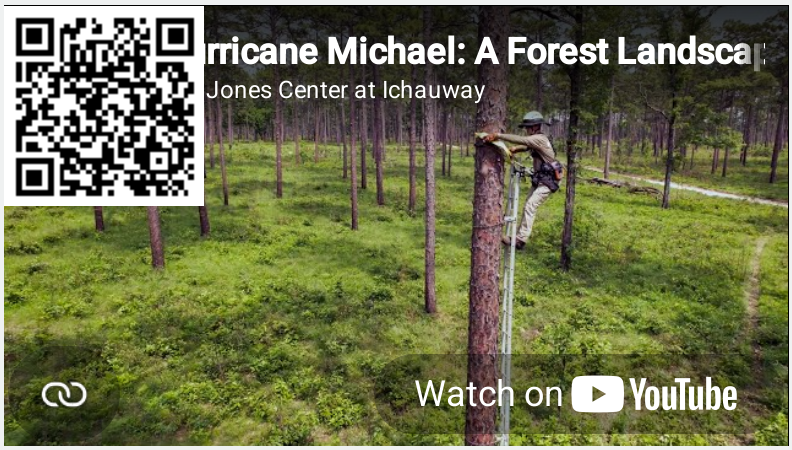


Figure 21.2.2: Process of landscape fragmentation. Fragmentation can be summarized in several different phases. Clockwise, from the upper left panel: (a) perforation (initial small openings), (b) dissection (larger intrusions of change, often along physical features), (c) dissipation (spread and coalescing of alteration), and eventually, (d) shrinkage (reduction of patch size), and attrition (loss of patches). © 2010 **Nature Education** Courtesy of Michigan Forests Forever Teachers Guide.

Video



Although there has been much research emphasis on how organisms respond to landscape heterogeneity, it is important to recognize that organisms comprise the heterogeneity, and often cause it themselves. For example, herbivores as different as bison (*Bison bison*) and prairie dogs (*Cynomys* spp.) influence large scale distribution of vegetation types and microhabitats in North American prairies. In natural systems, organisms may have the same ecosystem engineering effect as the pervasive influence of humans, although the effect of human influence has been the focus of far less attention in the development of landscape theory.

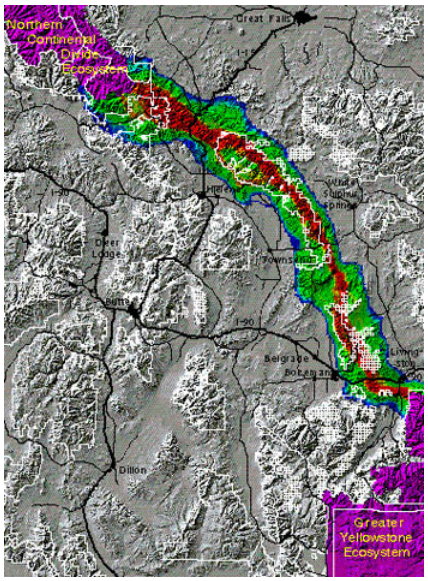


Figure 21.2.3: A corridor linking grizzly bear habitat in Montana, USA. This corridor was delineated based on grizzly bear habitat preferences and landscape structure. For conservation planning purposes it highlights the importance of protected national parks and forests. © 2010 Nature Education Courtesy of Richard Walker & Lance Craighead. All rights reserved.

Ecosystem and landscape scientists share a common interest in how spatial heterogeneity affects abiotic and biotic processes in ecosystems. Whether the compartments are abstract units of an ecosystem model or patches on a landscape, scientists are developing a unified framework to understand the dynamic flows of materials such as water, nutrients, and chemicals, both in time and space. The ideas can be applied to suggesting strategies for managing soil fertility and erosion, nutrient cycling, and pollution.

Video



Solving such problems requires the consideration of continuous environmental gradients, requiring the integration of approaches used in geomorphology, surface analysis, and spatial statistics. This interest has led to the emergence of a dynamic mosaic paradigm, which complements the patch-corridor-matrix paradigm. Landscape concepts regarding loss and fragmentation of vegetation cover around the world have become fundamental to understanding the carbon cycle, and predicting the consequences of global climate change.



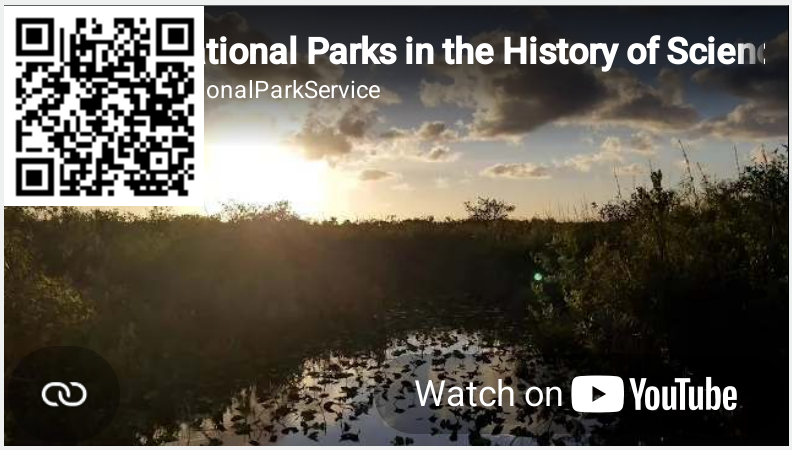
Figure 21.2.4: Schwerin, Germany. The interdependence of natural systems with human socio-economic systems in the landscape is illustrated. © 2010 **Nature Education** All rights reserved.

More than 75% of Earth's ice-free land shows evidence of alteration as a result of human residence and land use. Furthermore, the legacy of anthropogenic land use and natural events, like fire, is clearly important and has measurable effects on ecosystem function, even hundreds of years after landscape alteration. This anthropogenic scaling is fundamental to most ecological processes in this landscape. Natural processes that affect the stability and resilience of ecosystems apply equally well in wild lands and the vast majority of the biosphere where humans live (Figure 4). The challenge to landscape ecologists is to meld the ecology-centered spatial view with the society-centered holistic view to the benefit of understanding how spatial-temporal heterogeneity affects the resilience of the ecosystems of the earth on which all organisms depend.

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21.3: Island Biogeography

Video



Biogeography is the study of the distribution of species and ecosystems in geographic space and through geological time. Organisms and biological communities often vary in a regular fashion along geographic gradients of latitude, elevation, isolation, and habitat area. The latter pattern, often called the **species-area relationship**, has long been a fascination for biogeographers. Figure 21.3.1 demonstrates this species-area relationship for amphibians and reptiles in the West Indies. A study from around 1957 was included in Robert H. MacArthur and Edward O. Wilson's famous book "The Theory of Island Biogeography", and showed that among seven islands studied, the largest, Cuba, had the most species, and the smallest, Redonda, had the fewest. This general pattern has been found in many different islands groups, and across various different taxa.

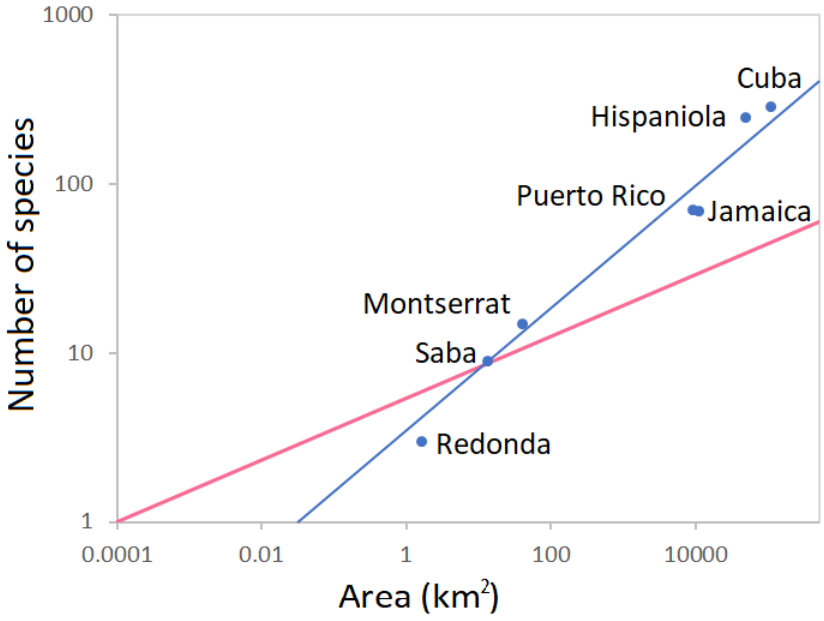


Figure 21.3.1: Species-area relationship for amphibians and reptilians on seven different islands in the West Indies. An original study (Darlington c. 1957), published in "The Theory of Island biogeography", showed a strong positive correlation between island size and number of species (blue line). A more recent study by Gao and Perry (2016) included data for many additional small

islands (smaller than Redonda) and found that while the pattern holds, the relationship is flatter than in the original study--indicated by the pink line. Figure drawn by Andy Wilson, based on Figure 4 in Gao and Perry (2016).

While studying these species-area relationships for their seminal book, MacArthur and Wilson were drawn to another of the four geographic gradients--that of isolation. They observed that some large Islands had fewer species than would be expected for their size, while conversely, some small islands had more species than expected.

While studying patterns of species richness on islands, two ecologists, Robert H. MacArthur and Edward O. Wilson, noted some exceptions to the **species-area relationship**. For example, some large islands had fewer species than expected due to their size, while some small islands had more species than expected. These patterns were explained by MacArthur and Wilson's **Equilibrium Theory of Island Biogeography**, which takes into account the fact that islands are colonized by species from elsewhere, and natural extinctions will occur on those islands, over long periods of time.

Video



Imagine there are two islands (**a** and **b**) located off the coast of the mainland. Although the two islands are about the same size, island **a** is located much farther away than island **b**. If you are a bird that lives on the mainland, which island are you most likely to find? The answer is generally island **b**. This means immigration (or colonization) is influenced by the distance of an island from the mainland (a source of colonists). Therefore, islands that are closer to the island are more likely to receive immigrants than islands that are further away.

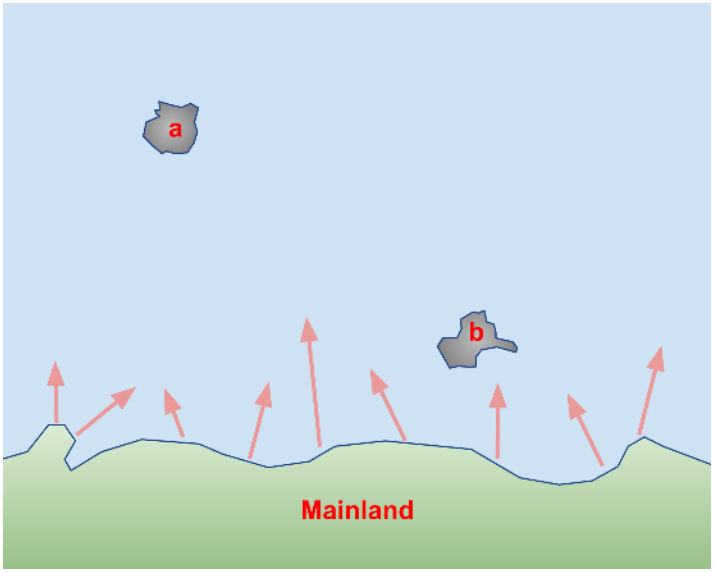


Figure 21.3.2: Two offshore islands--the Theory of Island Biogeography suggests that fewer species will colonize the more distant island **a**, in comparison to island **b** (credit: Andy Wilson, redrawn from Hdelucalowell15 [CC BY-SA 4.0 (https://creativecommons.org/licenses/by-sa/4.0)]

Once a species manages to reach and colonize an island, the rate of extinction is largely influenced by size of the island. This is because smaller islands tend to hold smaller populations (which are more likely to experience extinction due to stochastic effects like genetic drift). Larger habitat size reduces the probability of extinction of the colonized species due to chance events. Smaller islands are also likely to hold fewer populations in general because they have fewer resources and less diversity of resources. Larger islands have larger and more habitat areas, which typically leads to more differences in habitat or *habitat heterogeneity*. Higher heterogeneity means that there are more opportunities for a variety of species to find their suitable niches. Habitat heterogeneity also helps increase the number of species to successfully colonize after immigration.

Now let's consider the situation if we had two different islands sizes in our offshore archipelago, with **c** and **d**, much bigger than **a** and **b** Figure 21.3.3. We would expect extinction rates to be much lower on islands **c** and **d** than on the two smaller islands.

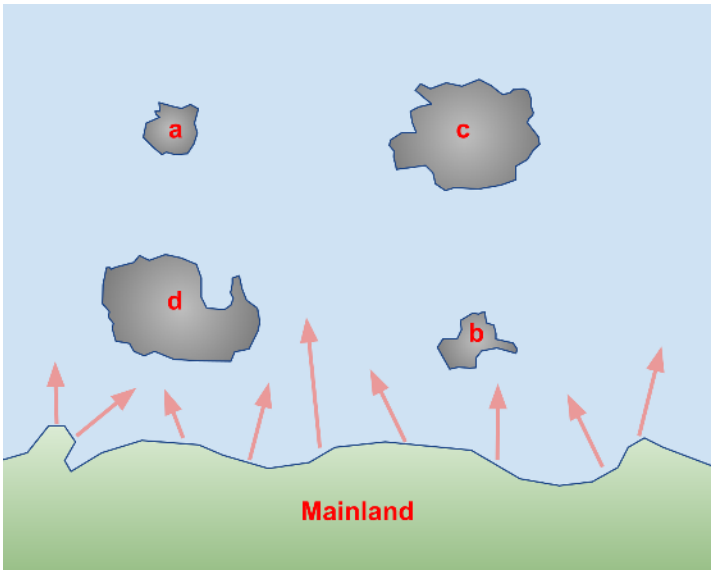


Figure 21.3.3: Four offshore islands--the Theory of Island Biogeography suggests that fewer species will go extinct on the larger islands **c** and **d**, in comparison to islands **a** and **b** (credit: Andy Wilson, redrawn from Wikipedia [CC BY-SA 4.0 (https://creativecommons.org/licenses/by-sa/4.0)]

We could plot both immigration and extinction relationships on a single image, as in Figure 21.3.4. Note the y-axis is the number of species (either colonizing or going extinct). Now we see that of the four islands in Figure 21.3.3, island **a** (small and far) would likely have the fewest species, island **d** (large and close), would have the most, and islands **b** and **c** would fall between the two extremes.

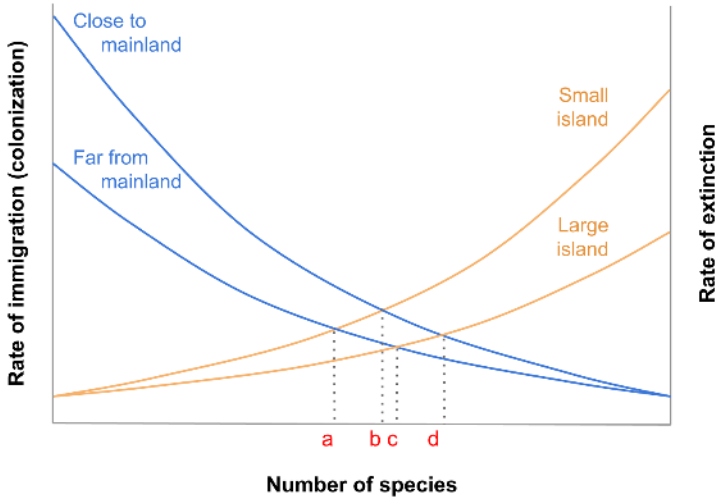


Figure 21.3.4: Equilibrium Theory of Island Biogeogaphy (credit: Andy Wilson, redrawn from Wikipedia [CC BY-SA 4.0 (https://creativecommons.org/licenses/by-sa/4.0)]

This basic graph makes a lot of assumptions but also offers a lot of insight. In this graph, immigration rates (blue lines) depend on proximity to mainland. Immigration rates also decline with species richness. That's becasuse its' easiest to immigrate to an island when it is empty because all the resources on the island are available. As the islands get more and more full, colonizing the island becomes more difficult.

Extinction rates (orange lines), as noted above, depend on island size. We also see that extinction rates tend to increase with the number of species. This should make sense: If there are no species on an island, extinction is impossible, but as more and more species arrive (and compete!) extinction becomes more likely.

Figure 21.3.2 shows the basic Equilibrium Theory of Island Biogeography. It suggests that islands will reach an equilibrium, or stable, number of species when immigration and extinction rates are equal! Note this model could be modified in multiple ways. Size of an island, for example, likely also impacts immigration rate (larger islands are easier to hit!), and islands that are close together may also share individuals (the Rescue effect!), but even this simple conceptualization has proven useful for understanding global species richness patterns.

One interesting point to note is that an equilibrium number of species is reached when immigration and extinction rates are equal, not when those processes stop! This means islands may consistently be changing species composition but should maintain fairly consistent levels of species richness. As odd as this sounds, early tests of the Equilibrium Theory of Island Biogeography supported these assumptions. When mangrove islands off the coast of Florida were fully cleared of their invertebrate (insect and arachnid) communities and allowed to recolonize, islands eventually stabilized with communities of about the same richness as they had before disturbance.

The island biogeography model has crucial applications for wildlife management because wildlife reserves or patches of habitat can be considered “islands” of habitat in “an ocean” of an inhabitable area. For this reason, the Theory Island Biogeography has become central to our understanding of how habitat fragmentation leads to biodiversity loss.

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CHAPTER OVERVIEW

Chapter 22: Biodiversity

Learning Objectives

- Differentiate among the types of biodiversity
- Learn how to measure diversity using indices
- Understand why biodiversity is not evenly distributed
- Learn how Rarefaction curves are used to estimate species richness

22.1: Introduction to Biodiversity
22.2: Importance of Biodiversity
22.3: The Biodiversity Crisis - HIPPPOC
22.4: Preserving Biodiversity
22.5: Measuring Biodiveristy
22.6: Patterns in Biodiversity

Summary

Genetic diversity, ecosystem diversity, and human-derived diversity are measures of biodiversity that currently define life on earth. Because it is often difficult to obtain a full list of species in any given location, various metrics are used to measure biodiversity, including Alpha, Beta, and Gamma diversity, and rarefaction curves. While around 2 million species have been scientifically described globally, estimates of the actual number of species on earth range from 10s of millions to billions.

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22.1: Introduction to Biodiversity

Introduction to Biodiversity

- Please read and watch the following Learning Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 1 hour.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Define biodiversity
- Explain what is meant by the 'biodiversity crisis'
- Provide examples of anthropogenic extinctions

Introduction

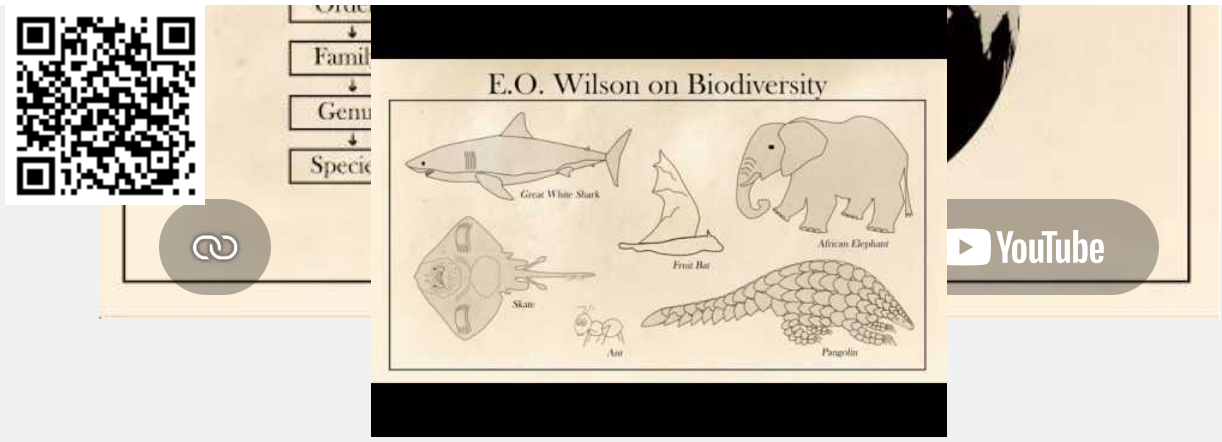
In the 1980s, biologists working in Lake Victoria in Africa discovered one of the most extraordinary products of evolution on the planet. Located in the Great Rift Valley, Lake Victoria (Figure 22.1.1) is a large lake about 68,900 km^2 in area (larger than Lake Huron, the second largest of North America's Great Lakes). Biologists were studying species of a family of fish called cichlids. They found that as they sampled for fish in different locations of the lake, they never stopped finding new species, and they identified nearly 500 evolved types of cichlids. But while studying these variations, they quickly discovered that the invasive Nile Perch was destroying the lake's cichlid population, bringing hundreds of cichlid species to extinction with devastating rapidity.



Figure 22.1.1: Cichlids are some of the most biodiverse fish on the planet but are also a casualty of devastating biodiversity loss. (credit: modification of work by Rishabh Tatiraju, using NASA World Wind software)

Video





Watch a 1-minute presentation by biologist E.O. Wilson (1929-2021) on the importance of biodiversity.

What is Biodiversity?

Biodiversity is a broad term for biological variety, and it can be measured at a number of organizational levels. Traditionally, ecologists have measured biodiversity by taking into account both the number of species and the number of individuals of each species (known as **relative abundance**). However, biologists are using different measures of biodiversity, including genetic diversity, to help focus efforts to preserve the biologically and technologically important elements of biodiversity.

Species Diversity

Scientists accept that the term biodiversity generally describes the number and kinds of species in a location or on the planet. This is known as **species diversity**. Species can be difficult to define, but most biologists still feel comfortable with the concept and are able to identify and count eukaryotic species in most contexts.

For example, the American Ornithologists' Union lists 2078 species of birds in North and Central America. This is one measure of the bird biodiversity on the continent. More sophisticated measures of diversity take into account the relative abundances of species. An ecologist analyzing a forest with 10 equally common species of trees would note that this first forest is more diverse than a forest that has the same 10 species of trees but where just one of those species makes up 95 percent of the trees.

In addition to these measures of species diversity, biologists have identified alternate measures of biodiversity, some of which are important in planning how to preserve biodiversity.

Genetic Diversity

One alternate concept of biodiversity, **genetic diversity**, is the raw material for evolutionary adaptation in a species and is represented by the variety of genes present within a population. A species' potential to adapt to changing environments or new diseases depends on this genetic diversity. The same is true for higher taxonomic categories. A genus with very different types of species will have more genetic diversity than a genus with species that look alike and have similar ecologies. If there were a choice between one of these genera of species being preserved, the one with the greatest potential for subsequent evolution is the most genetically diverse one. It would be ideal not to have to make such choices, but increasingly this may be the norm.

Beyond ecological importance, genetic diversity has potential benefits for humans as sources of pharmaceuticals, so it provides one way to measure diversity that is important to human health and welfare. Humans have also generated diversity through domestic animals, plants, and fungi. This diversity is suffering losses because of migration, market forces, and increasing globalism in agriculture, especially in heavily populated regions such as China, India, and Indonesia. The human population directly depends on this diversity as a stable food source, and its decline is troubling biologists and agricultural scientists.

Ecosystem Diversity

It is also useful to define **ecosystem diversity**, meaning the number of different ecosystems on the planet or in a given geographic area (Figure 22.1.2). Whole ecosystems can disappear even if some of the species might survive by adapting to other ecosystems. The loss of an ecosystem means the loss of interactions between species, the loss of unique features of coadaptation, and the loss of

biological productivity that an ecosystem is able to create. An example of a large, nearly extinct ecosystem in North America are the prairies (Figure 22.1.2*b*). Prairies once spanned central North America from the boreal forest in northern Canada down into Mexico. They are now all but gone, replaced by crop fields, pasture lands, and suburban sprawl. Many of the individual species survive but the hugely productive ecosystem as a whole has fallen apart. As a consequence, the most productive agricultural soils on the planet are disappearing or must be maintained at greater expense.

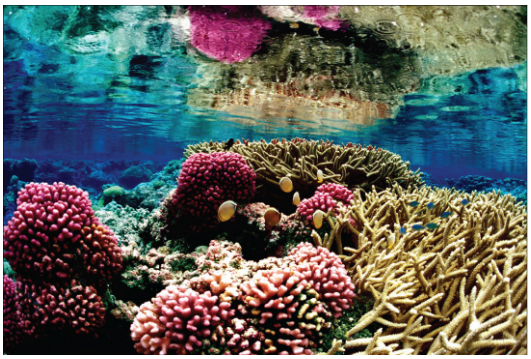



Figure 22.1.2: The variety of ecosystems on Earth—from (a) coral reef to (b) prairie—enables a great diversity of species to exist. (credit a: modification of work by Jim Maragos, USFWS; credit b: modification of work by Jim Minnerath, USFWS)

How Many Species?

As of August 2022, taxonomists have described nearly 2.3 million species that share this planet with us. While this total may seem impressive, available evidence suggests that this estimate vastly underestimates the true extent of Earth's biodiversity. In fact, even now, after all the exploration in years gone by, several thousand new species are described each year. Many new discoveries are made by skilled researchers recognizing new species by discerning variation in morphological characters; that includes the discoveries of a new small forest antelope from West Africa and a new species of shark off the coast of Mozambique. New genetic technologies have highlighted that there are many thousands of species yet to be described. Both traditional and genetic techniques rely heavily on the availability of specimens in Natural History Museums collections to help identify and describe new species. A lack of taxonomists and natural history collections in many of the world's most biodiverse countries means there is still a great deal of work to do.

The most exciting and newsworthy discoveries of new species generally involve higher-level taxa, especially living fossils. For example, in 1938, biologists across the world were stunned by the report of a strange fish caught in the Indian Ocean off South Africa. This fish, subsequently named *Latimeria chalumnae*, belongs to a group of marine fishes known as coelacanths that were common in ancient seas but were thought to have gone extinct 65 million years ago. Coelacanths are of interest to evolutionary biologists because they show certain features of muscles and bones in their fins that are comparable to the limbs of the first vertebrates that crawled onto land. Following the initial discovery, coelacanths have been found along Africa's Indian Ocean coast from South Africa to the Comoros and through to Kenya. Unfortunately, the entire coelacanth population, estimated at fewer than 500 individuals, is currently highly threatened because of ongoing fishing pressures.

Although field surveys have proven to be of great importance for discovering new species and populations, perhaps the greatest taxonomic progress has come from advances in genetic analyses which help to separate cryptic species previously lumped under more widespread species. For example, advances in genetic research recently highlighted that the African clawed frog *Xenopus laevis*—a popular model organism in biomedical research—consists of seven distinct species.

Molecular genetics and data processing and storage technologies are maturing to the point where cataloging the planet's species in an accessible way is close to feasible. DNA barcoding is one molecular genetic method, which takes advantage of rapid evolution in a mitochondrial gene present in eukaryotes, except the plants, to identify species using the sequence of portions of the gene. Plants are barcoded using a combination of chloroplast genes. Rapid mass sequencing machines make the molecular genetics portion of the work relatively inexpensive and quick. Computer resources store and make available large volumes of data. Projects are currently underway to use DNA barcoding to catalog museum specimens, which have already been named and studied, as well as testing the method on less studied groups. As of mid-2020, close to 750,000 named species had been barcoded. Early studies

suggest there are significant numbers of undescribed species that looked too much like sibling species to previously be recognized as different. These now can be identified with DNA barcoding.

Numerous computer databases now provide information about named species and a framework for adding new species. However, at the present rate of description of new species, it would still take close to 500 years before the complete catalog of life is known. Many, perhaps most, species on the planet do not have that much time given the **anthropogenic**, or human-caused, pressures on species around the world (Unit 5.2.3).

The presence of so many undiscovered species and communities makes precise estimates of species diversity incredibly difficult. Biologists' most recent estimates, combining genetic analysis of well-known groups with mathematical patterns, suggests there are between 1–6 billion distinct species on Earth, of which there are only about 163 million animals and 340 thousand plants. This is obviously much greater than the current catalog of around 2.3 million species.

Anthropogenic Extinctions

A review of the previous five mass extinctions can be found in Unit 3.3. The sixth, or Holocene, mass extinction appears to have begun earlier than previously believed and has mostly to do with the activities of *Homo sapiens*. Since the beginning of the Holocene period, there are numerous recent extinctions of individual species that are recorded in human writings. Most of these are coincident with the expansion of the European colonies since the 1500s.

Recent Extinctions

One of the earlier and popularly known examples is the dodo bird. The dodo bird lived in the forests of Mauritius, an island in the Indian Ocean. The dodo bird became extinct around 1662. It was hunted for its meat by sailors and was easy prey because the dodo, which did not evolve with humans, would approach people without fear. Introduced pigs, rats, and dogs brought to the island by European ships also killed dodo young and eggs (Figure 22.1.3).



Figure 22.1.3. The dodo bird was hunted to extinction around 1662. (credit: Ed Uthman, taken in Natural History Museum, London, England)

Steller's sea cow became extinct in 1768; it was related to the manatee and probably once lived along the northwest coast of North America. Steller's sea cow was first discovered by Europeans in 1741 and was hunted for meat and oil. The last sea cow was killed in 1768. That amounts to 27 years between the sea cow’s first contact with Europeans and extinction of the species.

In 1914, the last living passenger pigeon died in a zoo in Cincinnati, Ohio. This species had once darkened the skies of North America during its migrations, but it was hunted and suffered from habitat loss through the clearing of forests for farmland. In 1918, the last living Carolina parakeet died in captivity. This species was once common in the eastern United States, but it suffered from habitat loss. The species was also hunted because it ate orchard fruit when its native foods were destroyed to make way for farmland. The Japanese sea lion, which inhabited a broad area around Japan and the coast of Korea, became extinct in the 1950s due to fishermen. The Caribbean monk seal was distributed throughout the Caribbean Sea but was driven to extinction via hunting by 1952.

These are only a few of the recorded extinctions in the past 500 years.

The Red List

There is also the problem of understanding which species known to science are currently threatened and to what degree they are threatened. The International Union for Conservation of Nature (IUCN), an international non-profit, keeps a list of extinct and endangered species called the Red List, supported by scientific research. The list is not complete, but it describes 380 species of

vertebrates that went extinct after 1500 AD, 86 of which were driven extinct by overhunting or overfishing. In 2011, the list contained 61,000 species. It is categorized by taxonomy, type of threat, and other criteria (Figure 22.1.4).

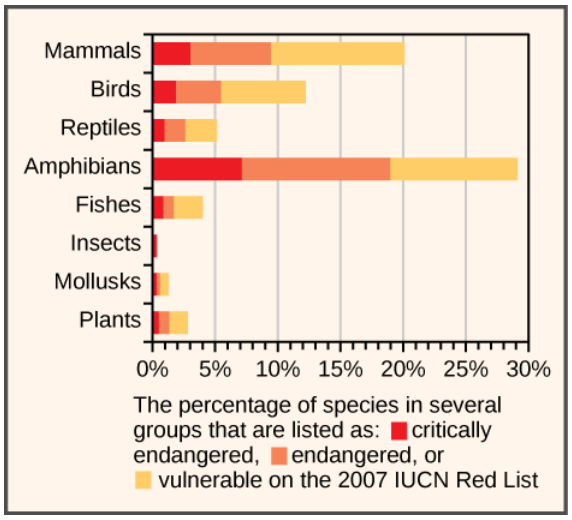


Figure 22.1.4: This chart shows the percentage of various animal species, by group, on the IUCN Red List as of 2007.

? Optional Activity 22.1.1

Which of the following statements is NOT supported by Figure 22.1.4?

A. There are more vulnerable fishes than critically endangered and endangered fishes combined.
B. There are more critically endangered amphibians than vulnerable, endangered, and critically endangered reptiles combined.
C. Within each group, there are more critically endangered species than vulnerable species.
D. A greater percentage of bird species are critically endangered than mollusk species.

Answer

C. Within each group, there are more critically endangered species than vulnerable species.

Evolution Connection: Lake Victoria cichlids

The Lake Victoria cichlids provide an example through which we can begin to understand biodiversity. The biologists studying cichlids in the 1980s discovered hundreds of cichlid species representing a variety of specializations to particular habitat types and specific feeding strategies: eating plankton floating in the water, scraping and then eating algae from rocks, eating insect larvae from the bottom, and eating the eggs of other species of cichlid. The cichlids of Lake Victoria are the product of adaptive radiation. Adaptive radiation is a rapid (less than three million years in the case of the Lake Victoria cichlids) branching through speciation of a phylogenetic tree into many closely related species; typically, the species “radiate” into different habitats and niches. The Galápagos finches are an example of a modest adaptive radiation with 15 species. The cichlids of Lake Victoria are an example of a spectacular adaptive radiation that includes about 500 species.

At the time biologists were making this discovery, some species began to quickly disappear. A culprit in these declines was a species of large fish that was introduced to Lake Victoria by fisheries to feed the people living around the lake. The Nile perch was introduced in 1963, but lay low until the 1980s when its populations began to surge. The Nile perch population grew by consuming cichlids, driving species after species to the point of extinction (the disappearance of a species). In fact, there were several factors that played a role in the extinction of perhaps 200 cichlid species in Lake Victoria: the Nile perch, declining lake water quality due to agriculture and land clearing on the shores of Lake Victoria, and increased fishing pressure. Scientists had not even cataloged all of the species present—so many were lost that were never named. The diversity is now a shadow of what it once was.

The cichlids of Lake Victoria are a thumbnail sketch of contemporary rapid species loss that occurs all over Earth and is caused by human activity. Extinction is a natural process of macroevolution that occurs at the rate of about one out of 1 million species

becoming extinct per year. The fossil record reveals that there have been five periods of mass extinction in history with much higher rates of species loss, and the rate of species loss today is comparable to those periods of mass extinction. However, there is a major difference between the previous mass extinctions and the current extinction we are experiencing: human activity. Specifically, three human activities have a major impact: the destruction of habitat, introduction of exotic species, and over-harvesting. Predictions of species loss within the next century, a tiny amount of time on geological timescales, range from 10 percent to 50 percent. Extinctions on this scale have only happened five other times in the history of the planet, and they have been caused by cataclysmic events that changed the course of the history of life in each instance. Earth is now in one of those times.

Estimates of Present-day Extinction Rates

Estimates of extinction rates are hampered by the fact that most extinctions are probably happening without being observed. The extinction of a bird or mammal is often noticed by humans, especially if it has been hunted or used in some other way. But there are many organisms that are less noticeable to humans (not necessarily of less value) and many that are undescribed.

The **background extinction rate** is estimated to be about 1 per million species years (E/MSY). One “species year” is one species in existence for one year. One million species years could be one species persisting for one million years, or a million species persisting for one year. If it is the latter, then one extinction per million species years would be one of those million species becoming extinct in that year. For example, if there are 10 million species in existence, then we would expect 10 of those species to become extinct in a year. This is the background rate.

One contemporary extinction-rate estimate uses the extinctions in the written record since the year 1500. For birds alone, this method yields an estimate of 26 E/MSY, almost three times the background rate. However, this value may be underestimated for three reasons. First, many existing species would not have been described until much later in the time period and so their loss would have gone unnoticed. Second, biologists know the number is higher than the written record suggests because now extinct species are being described from skeletal remains that were never mentioned in written history. And third, some species are probably already extinct even though conservationists are reluctant to name them as such. Taking these factors into account raises the estimated extinction rate to nearer 100 E/MSY. The predicted rate by the end of the century is 1500 E/MSY.

A second approach to estimating present-time extinction rates is to correlate species loss with habitat loss, and it is based on measuring forest-area loss and understanding species–area relationships. The species-area relationship is the rate at which new species are seen when the area surveyed is increased (Figure 22.1.5). Likewise, if the habitat area is reduced, the number of species seen will also decline. This kind of relationship is also seen in the relationship between an island’s area and the number of species present on the island: as one increases, so does the other, though not in a straight line.

Estimates of extinction rates based on habitat loss and species–area relationships have suggested that with about 90 percent of habitat loss an expected 50 percent of species would become extinct. Reducing forest area from 100 km^2 to 10 km^2, a decline of 90 percent, reduces the number of species by about 50 percent (Figure 22.1.5). Species–area estimates have led to estimates of present-day species extinction rates of about 1000 E/MSY and higher.

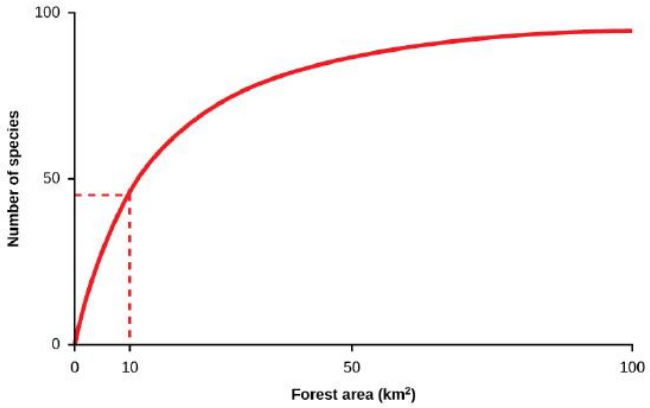


Figure 22.1.5. A typical species-area curve shows the cumulative number of species found as more and more area is sampled. The curve has also been interpreted to show the effect on species numbers of destroying habitat; a reduction in habitat of 90 percent from 100 km^2 to 10 km^2 reduces the number of species supported by about 50 percent.

Video





In this 9-minute video, discover why the current impacts of humans are as devastating to biodiversity as a large meteor.

Question after watching: What is lost when a species goes extinct? Consider all of the things that are lost, not just the biological ones.

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22.2: Importance of Biodiversity

Importance of Biodiversity

- Please read and watch the following Learning Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 1 hour.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Summarize the benefits of biodiversity

Introduction

It may not be clear why biologists are concerned about biodiversity loss. When biodiversity loss is thought of as the extinction of the passenger pigeon, the dodo bird, and even the woolly mammoth, the loss may appear to be an emotional one. However, is the loss practically important for the welfare of the human species? The loss of a keystone species can lead to ecological disaster and the extinction of many other species. But, from the perspective of evolution and ecology, the loss of one or two individual species may be relatively unimportant. Extinction is a normal part of macroevolution. Humans have accelerated the extinction rate, though, leading to losses of tens of thousands of species within our lifetimes. These losses are likely to have dramatic effects on human welfare through the collapse of ecosystems and added costs to maintain food production, clean air and water, and human health. There are strategies to avoid some of these losses and the field of study to preserve biodiversity is known as **conservation biology**.

Video



Watch this 4-minute video for an understanding of the importance of biodiversity.
Question after watching: Humans have cut and frayed the woven tapestry of Earth's biodiversity. List and describe three ways.

The Biodiversity Crisis

Biologists estimate that species extinctions are currently 500–1,000 times the normal, or **background**, rate seen previously in Earth's history. The current high rates will cause a precipitous decline in the biodiversity of the planet in the next century or two. The loss of biodiversity will include many species we know today. Although it is sometimes difficult to predict which species will

become extinct, many are listed as **endangered** (at great risk of extinction). However, many extinctions will affect species that biologists have not yet discovered.

Most of these “invisible” species that will become extinct currently live in tropical rainforests like those of the Amazon basin or on coral reefs. Rainforests are the most diverse terrestrial ecosystems on the planet and are being destroyed rapidly by deforestation (Figure 22.2.1). Between 1970 and 2011, almost 20 percent of the Amazon rainforest was lost. Coral reefs are being lost to overharvesting, warming oceans, and pollution.



Figure 22.2.1. This tropical lowland rainforest in Madagascar is an example of a high biodiversity habitat. This particular location is protected within a national forest, yet only 10 percent of the original coastal lowland forest remains, and research suggests half the original biodiversity has been lost. (credit: Frank Vassen)

Biodiversity loss refers to the reduction of biodiversity due to displacement or extinction of species. The loss of a particular individual species may seem unimportant to some, especially if it is not a **charismatic species** like the Bengal tiger or the bottlenose dolphin. However, the current accelerated extinction rate means the loss of tens of thousands of species within our lifetimes. Much of this loss is occurring in tropical rainforests as mentioned above, which are very high in biodiversity but are being cleared for timber and agriculture. This is likely to have dramatic effects on human welfare through the collapse of ecosystems.

Biologists recognize that human populations are embedded in ecosystems and are dependent on them, just as is every other species on the planet. Agriculture began after early hunter-gatherer societies first settled in one place and heavily modified their immediate environment. This cultural transition has made it difficult for many modern humans to recognize their dependence on living things other than crops and domesticated animals on the planet. Today our technology smooths out the harshness of existence and allows many of us to live longer, more comfortable lives, but ultimately the human species cannot exist without its surrounding ecosystems. Our ecosystems provide us with food, medicine, clean air and water, recreation, and spiritual and aesthetical inspiration.

Current Species Diversity

Despite considerable effort, knowledge of the species that inhabit the planet is limited. A recent estimate suggests that only 13% of eukaryotic species have been named (Table 1). Estimates of numbers of prokaryotic species are largely guesses, but biologists agree that science has only just begun to catalog their diversity. Some scientists estimate that there may be over 100 million species of prokaryotes alone. Given that Earth is losing species at an accelerating pace, science knows little about what is being lost.

Table 1. This table shows the estimated number of species by taxonomic group—including both described (named and studied) and predicted (yet to be named) species.

Estimated Numbers of Described and Predicted species						
	Source: Mora et al 2011		Source: Chapman 2009		Source: Groombridge and Jenkins 2002	
	Described	Predicted	Described	Predicted	Described	Predicted
Animals	1,124,516	9,920,000	1,424,153	6,836,330	1,225,500	10,820,000
Photosynthetic protists	17,892	34,900	25,044	200,500	—	—
Fungi	44,368	616,320	98,998	1,500,000	72,000	1,500,000
Plants	224,244	314,600	310,129	390,800	270,000	320,000
Non-photosynthetic protists	16,236	72,800	28,871	1,000,000	80,000	600,000
Prokaryotes	—	—	10,307	1,000,000	10,175	—
Total	1,438,769	10,960,000	1,897,502	10,897,630	1,657,675	13,240,000

There are various initiatives to catalog described species in accessible and more organized ways, and the internet is facilitating that effort. Nevertheless, at the current rate of species description, which according to the State of Observed Species reports is 17,000–20,000 new species a year, it would take close to 500 years to describe all of the species currently in existence. The task, however, is becoming increasingly impossible over time as extinction removes species from Earth faster than they can be described.

Naming and counting species may seem an unimportant pursuit given the other needs of humanity, but it is not simply an accounting. Describing species is a complex process by which biologists determine an organism's unique characteristics and whether or not that organism belongs to any other described species. It allows biologists to find and recognize the species after the initial discovery to follow up on questions about its biology. That subsequent research will produce the discoveries that make the species valuable to humans and to our ecosystems. Without a name and description, a species cannot be studied in depth and in a coordinated way by multiple scientists.

Patterns of Biodiversity

Biodiversity is not evenly distributed on the planet. Lake Victoria contained almost 500 species of cichlids (just one family of fishes that are present in the lake) before the introduction of an exotic species in the 1980s and 1990s caused a mass extinction. All of these species were found only in Lake Victoria, which is to say they were endemic. Endemic species with highly restricted distributions, like the ciclids, are particularly vulnerable to extinction.

Lake Huron contains about 79 species of fish, all of which are found in many other lakes in North America. What accounts for the difference in diversity between Lake Victoria and Lake Huron? Lake Victoria is a tropical lake, while Lake Huron is a temperate lake. Lake Huron in its present form is only about 7,000 years old, while Lake Victoria in its present form is about 15,000 years old. These two factors, latitude and age, are two of several hypotheses biogeographers have suggested to explain biodiversity patterns on Earth.

Biogeography is the study of the distribution of the world's species both in the past and in the present (Unit 4.4.5). The work of biogeographers is critical to understanding our physical environment, how the environment affects species, and how changes in environment impact the distribution of a species.

There are three main fields of study under the heading of biogeography: ecological biogeography, historical biogeography (called paleobiogeography), and conservation biogeography. Ecological biogeography studies the current factors affecting the distribution of plants and animals. Historical biogeography, as the name implies, studies the past distribution of species. Conservation biogeography, on the other hand, is focused on the protection and restoration of species based upon the known historical and current ecological information.

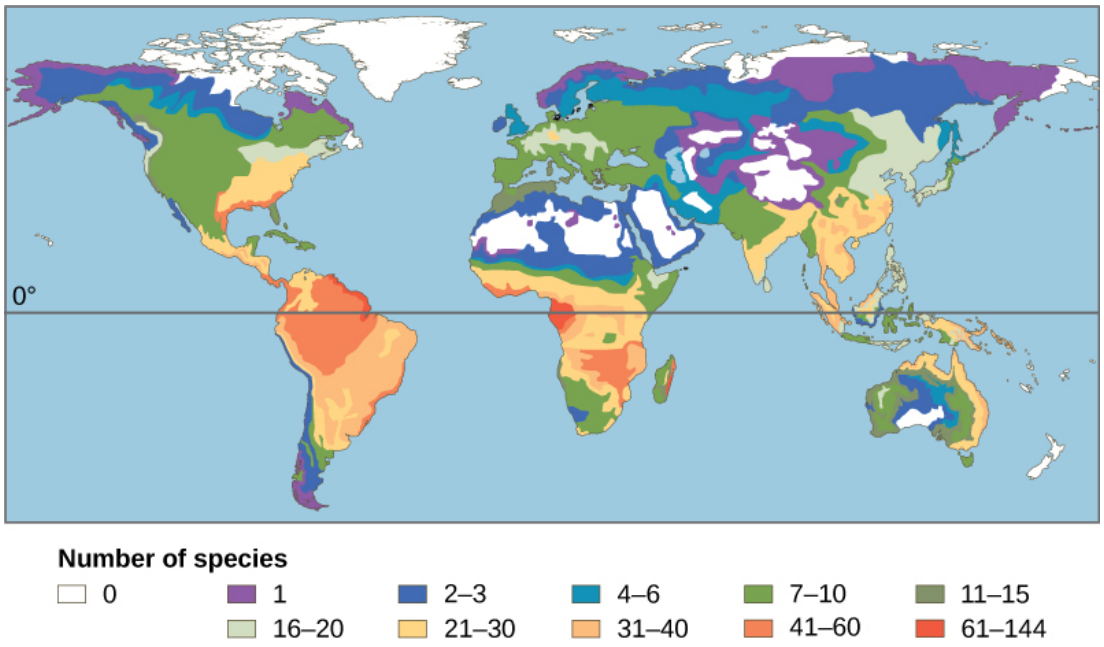


Figure 22.2.3. This map illustrates the number of amphibian species across the globe and shows the trend toward higher biodiversity at lower latitudes. A similar pattern is observed for most taxonomic groups.

One of the oldest observed patterns in ecology is that biodiversity typically increases as latitude decreases. In other words, biodiversity increases closer to the equator (Figure 22.2.3).

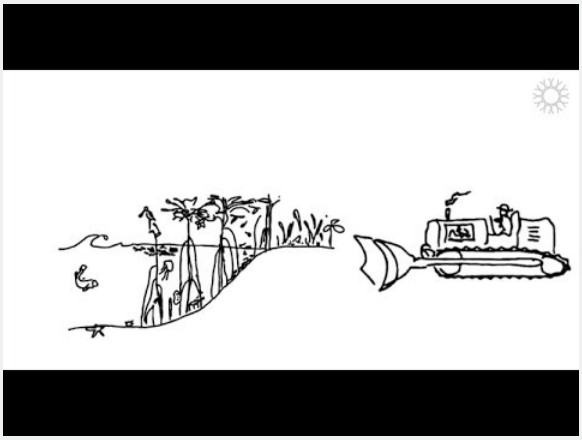
It is not yet clear why biodiversity increases closer to the equator, but hypotheses include the greater age of the ecosystems in the tropics versus temperate regions, which were largely devoid of life or drastically impoverished during the last ice age. The greater age provides more time for speciation, the evolutionary process of creating new species. Another possible explanation is the greater energy the tropics receive from the sun. But scientists have not been able to explain how greater energy input could translate into more species. The complexity of tropical ecosystems may promote speciation by increasing the habitat complexity, thus providing more ecological niches. Lastly, the tropics have been perceived as being more stable than temperate regions, which have a pronounced climate and day-length seasonality. The stability of tropical ecosystems might promote speciation. Regardless of the mechanisms, it is certainly true that biodiversity is greatest in the tropics. There are also high numbers of endemic species.

Importance of Biodiversity

Loss of biodiversity may have reverberating consequences on ecosystems because of the complex interrelations among species. For example, the extinction of one species may cause the extinction of another. Biodiversity is important to the survival and welfare of human populations because it has impacts on our health and our ability to feed ourselves through agriculture and harvesting populations of wild animals. Much of the importance of biodiversity comes from what is known as **ecosystem services** (Unit 5.2.3).

Video





In this 9-minute video by the California Academy of Sciences, the many ecosystem services that biodiversity provides are described.

Question after watching: Describe three different services and several examples of how biodiversity is important to humans.

Health

Many medications are derived from natural chemicals made by a diverse group of organisms. For example, many plants produce compounds meant to protect the plant from insects and other animals that eat them. Some of these compounds also work as human medicines. Contemporary societies that live close to the land often have a broad knowledge of the medicinal uses of plants growing in their area. For centuries in Europe, older knowledge about the medical uses of plants was compiled in herbals—books that identified the plants and their uses. Humans are not the only animals to use plants for medicinal reasons. The other great apes, orangutans, chimpanzees, bonobos, and gorillas as well as many other organisms such as elephants, bees, lizards, and canids have all been observed self-medicating with plants.

Modern pharmaceutical science also recognizes the importance of these plant compounds. Examples of significant medicines derived from plant compounds include aspirin (from the white willow, *Salix alba*), codeine (from the poppy, *Papaver somniferum*), digoxin (from the genus *Digitalis)*, atropine (from the belladonna, *Atropa belladonna)*, and vincristine (Figure 22.2.4). Many medications were once derived from plant extracts but are now synthesized. It is estimated that, at one time, 25 percent of modern

drugs contained at least one plant extract. That number has probably decreased to about 10 percent as natural plant ingredients are replaced by synthetic versions of the plant compounds. Antibiotics, which are responsible for extraordinary improvements in health and lifespans in developed countries, are compounds largely derived from fungi and bacteria.



Figure 22.2.4. *Catharanthus roseus*, the Madagascar periwinkle, has various medicinal properties. Among other uses, it is a source of vincristine, a drug used in the treatment of lymphomas. (credit: Forest and Kim Starr)

In recent years, animal venoms and poisons have excited intense research for their medicinal potential. By 2007, the FDA had approved five drugs based on animal toxins to treat diseases such as hypertension, chronic pain, and diabetes. Another five drugs are undergoing clinical trials and at least six drugs are being used in other countries. Other toxins under investigation come from mammals, snakes, lizards, various amphibians, fish, snails, octopuses, and scorpions.

Aside from representing billions of dollars in profits, these medications improve people's lives. Pharmaceutical companies are actively looking for new natural compounds that can function as medicines. It is estimated that more than 30% of pharmaceutical research and development is spent on natural compounds and that about 35% of new drugs brought to market between 1981 and 2002 were from natural compounds.

Agriculture

Since the beginning of human agriculture more than 10,000 years ago, human groups have been breeding and selecting crop varieties. This crop diversity matched the cultural diversity of highly subdivided populations of humans. For example, potatoes were domesticated beginning around 7,000 years ago in the central Andes of Peru and Bolivia. The potatoes grown in that region belong to seven species and the number of varieties likely is in the thousands. Each variety has been bred to thrive at particular elevations and soil and climate conditions. The diversity is driven by the diverse demands of the topography, the limited movement of people, and the demands created by crop rotation for different varieties that will do well in different fields.

Potatoes are only one example of human-generated diversity. Every plant, animal, and fungus that has been cultivated by humans has been bred from original wild ancestor species into diverse varieties arising from the demands for food value, adaptation to growing conditions, and resistance to pests. The potato demonstrates a well-known example of the risks of low crop diversity: the tragic Irish potato famine when the single variety grown in Ireland became susceptible to potato blight, wiping out the crop. The loss of the crop led to famine, death, and mass emigration. Resistance to disease is a chief benefit to maintaining crop biodiversity, and the lack of diversity in contemporary crop species carries similar risks. Seed companies, which are the source of most crop varieties in developed countries, must continually breed new varieties to keep up with evolving pest organisms. These same seed companies, however, have participated in the decline of the number of varieties available as they focus on selling fewer varieties in more areas of the world.

The ability to create new crop varieties relies on the diversity of varieties available and the accessibility of wild forms related to the crop plant. These wild forms are often the source of new gene variants that can be bred with existing varieties to create varieties with new attributes. Loss of wild species related to a crop will mean the loss of potential in crop improvement. Maintaining the genetic diversity of wild species related to domesticated species ensures our continued food supply.

Since the 1920s, government agriculture departments have maintained seed banks of crop varieties as a way to maintain crop diversity. This system has flaws because, over time, seed banks are lost through accidents, and there is no way to replace them. In 2008, the Svalbard Global Seed Vault (Figure 22.2.5) began storing seeds from around the world as a backup system to the regional

seed banks. If a regional seed bank stores varieties in Svalbard, losses can be replaced from Svalbard. The seed vault is located deep into the rock of an arctic island. Conditions within the vault are maintained at ideal temperature and humidity for seed survival, but the deep underground location of the vault in the arctic means that failure of the vault's systems will not compromise the climatic conditions inside the vault.



Figure 22.2.5. The Svalbard Global Seed Vault is a storage facility for seeds of Earth's diverse crops. (credit: Mari Tefre, Svalbard Global Seed Vault)

? Optional Activity 22.2.1

Figure 22.2.5: The Svalbard Global Seed Vault is located on Spitsbergen island in Norway, which has an arctic climate. Why might an arctic climate be good for seed storage?

Answer

The ground is permanently frozen so the seeds will keep even if the electricity fails.

Crop success is largely dependent on the quality of the soil. Although some agricultural soils are rendered sterile using controversial cultivation and chemical treatments, most contain a huge diversity of organisms that maintain nutrient cycles—breaking down organic matter into nutrient compounds that crops need for growth. These organisms also maintain soil texture that affects water and oxygen dynamics in the soil that are necessary for plant growth. If farmers had to maintain arable soil using alternate means, the cost of food would be much higher than it is now. These kinds of processes are called ecosystem services. They occur within ecosystems, such as soil ecosystems, as a result of the diverse metabolic activities of the organisms living there, but they provide benefits to human food production, drinking water availability, and breathable air.

Other key ecosystem services related to food production are plant pollination and crop pest control. Over 150 crops in the United States require pollination to produce. One estimate of the benefit of honeybee pollination within the United States is $1.6 billion per year; other pollinators contribute up to $6.7 billion more.

Many honeybee populations are managed by apiarists who rent out their hives' services to farmers. Honeybee populations in North America have been suffering large losses caused by a syndrome known as colony collapse disorder, whose cause is unclear. Other pollinators include a diverse array of other bee species and various insects and birds. Loss of these species would make growing crops requiring pollination impossible, increasing dependence on other crops.

Finally, humans compete for their food with crop pests, most of which are insects. Pesticides control these competitors; however, pesticides are costly and lose their effectiveness over time as pest populations adapt. They also lead to collateral damage by killing non-pest species and risking the health of consumers and agricultural workers. Ecologists believe that the bulk of the work in removing pests is actually done by predators and parasites of those pests, but the impact has not been well studied. A review found that in 74 percent of studies that looked for an effect of landscape complexity on natural enemies of pests, the greater the complexity, the greater the effect of pest-suppressing organisms. An experimental study found that introducing multiple enemies of pea aphids (an important alfalfa pest) increased the yield of alfalfa significantly. This study shows the importance of landscape diversity via the question of whether a diversity of pests is more effective at control than one single pest; the results showed this to be the case. Loss of diversity in pest enemies will inevitably make it more difficult and costly to grow food.

Optional Activity 22.2.2

Which of the following agricultural crops is most likely to survive a catastrophic event?

A. a monoculture of a crop on a large surface
B. diverse varieties of a crop surrounded by a diverse ecosystem
C. a single crop surrounded by a diverse ecosystem
D. diverse varieties of a crop in a simple ecosystem

Answer

B. diverse varieties of a crop surrounded by a diverse ecosystem.

Video



In this short 1.5-minute video, learn how biodiversity for food and agriculture is indispensable to food security, sustainable development, and the supply of many vital ecosystem services.
Question after watching: In what ways could you diversify your own diet and support local food growers?

Wild Food Sources

In addition to growing crops and raising food animals, humans obtain food resources from wild populations, primarily wild fish populations. For about one billion people, aquatic resources provide the main source of animal protein. But since 1990, production from global fisheries has declined. Despite considerable effort, few fisheries on Earth are managed sustainability.

Fishery extinctions rarely lead to complete extinction of the harvested species, but rather to a radical restructuring of the marine ecosystem in which a dominant species is so over-harvested that it becomes a minor player, ecologically. In addition to humans losing a food source, these alterations affect many other species in ways that are difficult or impossible to predict. The collapse of fisheries has dramatic and long-lasting effects on local human populations that work in the fishery. In addition, the loss of an inexpensive protein source to populations that cannot afford to replace it will increase the cost of living and limit societies in other ways. In general, the fish taken from fisheries have shifted to smaller species and the larger species are overfished. The ultimate outcome could clearly be the loss of aquatic systems as food sources.

Psychological and Moral Value

Finally, it has been argued that humans benefit psychologically from living in a biodiversity world. The chief proponent of this idea was famed entomologist E. O. Wilson. He argued that human evolutionary history has adapted us to living in a natural environment and that built environments generate stresses that affect human health and well-being. There is considerable research into the psychologically regenerative benefits of natural landscapes that suggest the hypothesis may hold some truth. In addition, there is a moral argument that humans have a responsibility to inflict as little harm as possible on other species.

Video



This 5.5-minute video from the EU's Science for Environment Policy summarizes many of the ecosystem services and benefits discussed above.

Question after watching: What is your opinion of using monetary values for nature to convince people to preserve or restore natural systems?

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22.3 - The Biodiversity Crisis - HIPPPOC

- Please read and watch the following Learning Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 1.5 hours.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Identify and explain the major causes of anthropogenic global change and their impacts on biodiversity.

Introduction

The core threat to biodiversity on the planet, and therefore a threat to human welfare, is the combination of human population growth and the resources used by that population. The human population requires resources to survive and grow, and many of those resources are being removed unsustainably from the environment. The three greatest proximate threats to biodiversity are habitat loss, overexploitation (also known as overharvesting), pollution, predator losses, and introduction of invasive species. These are a direct result of human population growth, resource use, increased mobility, and trade. One of the major causes of extinction, **anthropogenic climate change**, is covered in more depth later in the course.

Together, these threats are known as **HIPPPOC**: **h**abitat loss, **i**nvasive species, **p**ollution, **p**opulation (human), **p**redator loss, **o**verexploitation, and **c**limate change.

Habitat Loss

Humans rely on technology to modify their environment and make it habitable. Other species cannot do this. Elimination of their habitat—whether it is a forest, coral reef, grassland, or flowing river—will kill the individuals in the species. Remove the entire habitat and the species will become extinct, unless they are among the few species that do well in human-built environments. Human destruction of habitats accelerated in the latter half of the twentieth century.

Consider the exceptional biodiversity of Sumatra: it is home to one species of orangutan, a species of critically endangered elephant, and the Sumatran tiger, but half of Sumatra's forest is now gone. The neighboring island of Borneo, home to the other species of orangutan, has lost a similar area of forest. Forest loss continues in protected areas of Borneo. The orangutan in Borneo is listed as endangered by the International Union for Conservation of Nature (IUCN), but it is simply the most visible of thousands of species that will not survive the disappearance of the forests of Borneo. The forests are removed for timber and to plant palm oil plantations (Figure 22.3.1). Palm oil is used in many products including food products, cosmetics, and biodiesel in Europe. A 5-year estimate of global forest cover loss for the years from 2000 to 2005 was 3.1%. Much loss (2.4%) occurred in the tropics where forest loss is primarily from timber extraction. These losses certainly also represent the extinction of species unique to those areas.



(a) (b)



(c)



(d) (e)

Figure 22.3.1: (a) One species of orangutan, *Pongo pygmaeus*, is found only in the rainforests of Borneo, and the other species of orangutan (*Pongo abelii*) is found only in the rainforests of Sumatra. These animals are examples of the exceptional biodiversity of (c) the islands of Sumatra and Borneo. Other species include the (b) Sumatran tiger (*Panthera tigris sumatrae*) and the (d) Sumatran elephant (*Elephas maximus sumatranus*), both critically endangered species. Rainforest habitat is being removed to make way for (e) oil palm plantations such as this one in Borneo's Sabah Province. (credit a: modification of work by Thorsten Bachner; credit b: modification of work by Dick Mudde; credit c: modification of work by U.S. CIA World Factbook; credit d: modification of work by "Nonprofit Organizations"/Flickr; credit e: modification of work by Dr. Lian Pin Koh)

Preventing Habitat Destruction with Wise Wood Choices

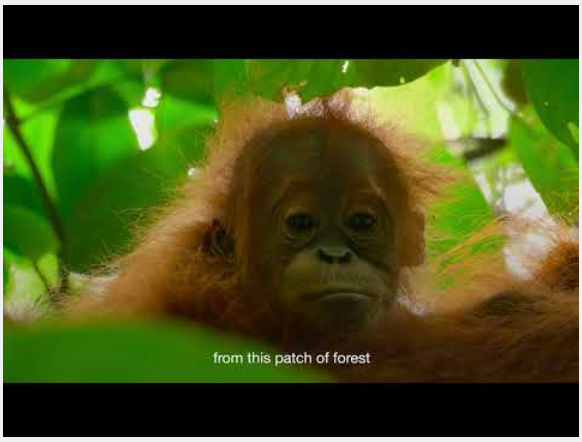
Most consumers do not imagine that the home improvement products they buy might be contributing to habitat loss and species extinctions. Yet the market for illegally harvested tropical timber is huge, and the wood products often find themselves in building supply stores. How is it possible to determine if a wood product, such as flooring, was harvested sustainably or even legally?

Various certifications can identify sustainably harvested forest products. Looking for certifications on flooring and other hardwood products is one way to ensure that the wood has not been taken illegally from a tropical forest. Some of these certifications are run by timber companies, however, thus creating a conflict of interest. Another approach is to buy domestic wood species. While it would be great if there was a list of legal versus illegal woods, it is not that simple. Logging and forest management laws vary from country to country; what is illegal in one country may be legal in another. Where and how a product is harvested and whether the forest from which it comes is being sustainably maintained all factor into whether a wood product will be certified. It is always a good idea to ask questions about where a wood product came from and how the supplier knows that it was harvested legally.

Habitat destruction can affect ecosystems other than forests. Rivers and streams are important ecosystems and are frequently the target of habitat modification. Damming of rivers affects flow and access to habitat. Altering a flow regime can reduce or eliminate populations that are adapted to seasonal changes in flow. Many fish species, including salmon, have seen declines caused by river damming and habitat loss.

Research has confirmed that species of amphibians that must carry out parts of their life cycles in both aquatic and terrestrial habitats are at greater risk of population declines and extinction because of the increased likelihood that one of their habitats or access between them will be lost. This is of particular concern because amphibians have been declining in numbers and going extinct more rapidly than many other groups for a variety of possible reasons.





Foresters identify strategies to manage forest habitats sustainably by mimicking natural processes in this 3.5-minute video from the World Wildlife Fund.
Question after watching: What are benefits to sustainable logging as described in the video?

Invasive Species

Non-native species are those that have been intentionally or unintentionally introduced by humans into an ecosystem in which they did not evolve. Human transportation of people and goods, including the intentional transport of organisms for trade, has dramatically increased the introduction of species into new ecosystems. These new introductions are often at distances that are well beyond the capacity of the species to ever travel on its own, and outside the range of the species' natural predators.

Most non-native species introductions probably fail because of the low number of individuals introduced or poor adaptation to the ecosystem they enter. Some species, however, have characteristics that can make them especially successful in a new ecosystem. These non-native species may undergo dramatic population increases in their new habitat and reset the ecological conditions in the new environment, threatening the native species that already exist there. When this happens, the non-native species is termed an **invasive species**. Invasive species can threaten other species through competition for resources, increased predation, or by causing new diseases.

Many invasive species are well suited evolutionarily to exploiting human transportation as a means to migrate, whether by air, sea, or land. The accidental introduction of the brown tree snake via aircraft (Figure 22.3.2) from the Solomon Islands to Guam in 1950 led to the extinction of three species of birds and three to five species of reptiles endemic to the island. Several other species are

still threatened. Islands do not make up a large area of land on the globe, but they do contain a disproportionate number of endemic species because of their isolation from mainland ancestors.

Lakes and islands are particularly vulnerable to extinction threats from non-native species. In Lake Victoria, the intentional introduction of the Nile perch was largely responsible for the extinction of about 200 species of cichlids. Many introductions of aquatic species, both marine and freshwater, have occurred when ships have dumped ballast water taken on at a port of origin into waters at a destination port. Water from the port of origin is pumped into tanks on a ship empty of cargo to increase stability. The water is drawn from the ocean or estuary of the port and typically contains living organisms such as plant parts, microorganisms, eggs, larvae, or aquatic animals. The water is then pumped out before the ship takes on cargo at the destination port, which may be on a different continent.

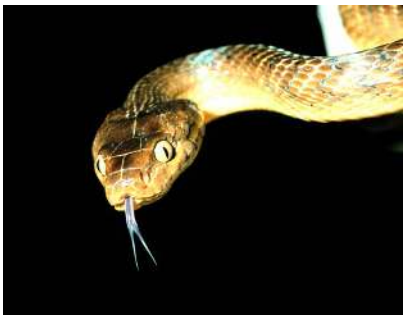


Figure 22.3.2. The brown tree snake, *Boiga irregularis*, is an exotic species that has caused numerous extinctions on the island of Guam since its accidental introduction in 1950. (credit: NPS)

Invading exotic species can also be disease organisms. It now appears that the global decline in amphibian species recognized in the 1990s is, in some part, caused by the fungus *Batrachochytrium dendrobatidis*, which causes the disease chytridiomycosis (Figure 22.3.3). There is evidence that the fungus is native to Africa and may have been spread throughout the world by transport of a commonly used laboratory and pet species: the African clawed frog, *Xenopus laevis*. It may well be that biologists themselves are responsible for spreading this disease worldwide. The North American bullfrog, *Rana catesbeiana*, which has also been widely introduced as a food animal but which easily escapes captivity, survives most infections of *B. dendrobatidis* and can act as a reservoir for the disease.



Figure 22.3.3. This Limosa harlequin frog (*Atelopus limosus*), an endangered species from Panama, died from a fungal disease called chytridiomycosis. The red lesions are symptomatic of the disease. (credit: Brian Gratwicke)

Video





In this 5-minute video, discover the devastating impact that invasive species can have on ecosystems. Question after watching: Do some research to find out what invasive species are a problem in your area? What is being done to combat them?

Optional Activity 22.3.1

Invasive predator species are especially threatening to what kind of ecosystem?

A. deserts
B. marine ecosystems
C. islands
D. tropical forests

Answer

C. islands

Pollution

Air Pollution

Air pollution occurs in many forms but can generally be thought of as gaseous and particulate contaminants that are present in the earth's atmosphere. Chemicals discharged into the air that have a direct impact on the environment are called **primary pollutants**. These primary pollutants sometimes react with other chemicals in the air to produce **secondary pollutants**.

Outdoor air pollution involves exposures that take place outside of the built environment. Examples include fine particles produced by the burning of coal, noxious gases such as sulfur dioxide, nitrogen oxides and carbon monoxide; ground-level ozone and tobacco smoke. **Indoor air pollution** involves exposures to particulates, carbon oxides, and other pollutants carried by indoor air or dust. Examples include household products and chemicals, out-gassing of building materials, allergens (cockroach and mouse dropping, mold, pollen), and tobacco smoke.

A **point source** of air pollution refers to an emission source that does not move including factories, power plants, and dry cleaners. The term **non-point sources** is used to describe many sources of air pollution located together whose individual emissions may be below thresholds of concern, but whose collective emissions can be significant. Non-point sources include the construction of housing developments, runoff from asphalt, and landfills. In crop production, the misapplication of fertilizers, herbicides, and pesticides can potentially result in aerial drift of these materials and harm may be caused.

Video



In this 4-minute video from National Geographic, learn how greenhouse gasses, smog, and toxic pollutants affect climate change and human health.

Question after watching: What strategies beyond those discussed in the video do you think will help to reduce air pollution?

Unlike the above-mentioned sources of air pollution, air pollution caused by **natural sources** is not caused by people or their activities. An erupting volcano emits particulate matter and gases, forest and prairie fires can emit large quantities of pollutants, dust storms can create large amounts of particulate matter, and plants and trees naturally emit volatile organic compounds which can form aerosols that can cause a natural blue haze.

Water Pollution

Water pollution is the contamination of water by an excess amount of a substance that can cause harm to human beings and/or the ecosystem. The level of water pollution depends on the abundance of the pollutant, the ecological impact of the pollutant, and the use of the water. Pollutants are derived from biological, chemical, or physical processes. Although natural processes such as volcanic eruptions or evaporation sometimes can cause water pollution, most pollution is derived from human, land-based activities (Figure 22.3.4).



Figure 22.3.4. Water Pollution. Obvious water pollution in the form of floating debris, largely plastics; microscopic and chemical water pollutants are often much more harmful than visible ones. Source: Stephen Codrington at Wikimedia Commons

Water pollutants can move through different water reservoirs, as the water carrying them progresses through stages of the water cycle (Figure 22.3.5). **Water residence time** (the average time that a water molecule spends in a water reservoir) is very important to pollution problems because it affects pollution potential. Water in rivers has a relatively short residence time, so pollution usually is there only briefly. Of course, pollution in rivers may simply move to another reservoir, such as the ocean, where it can cause further problems. Groundwater is typically characterized by slow flow and longer residence time, which can make groundwater pollution particularly problematic. Finally, **pollution residence time** can be much greater than the water residence time because a pollutant may be taken up for a long time within the ecosystem or absorbed onto sediment.

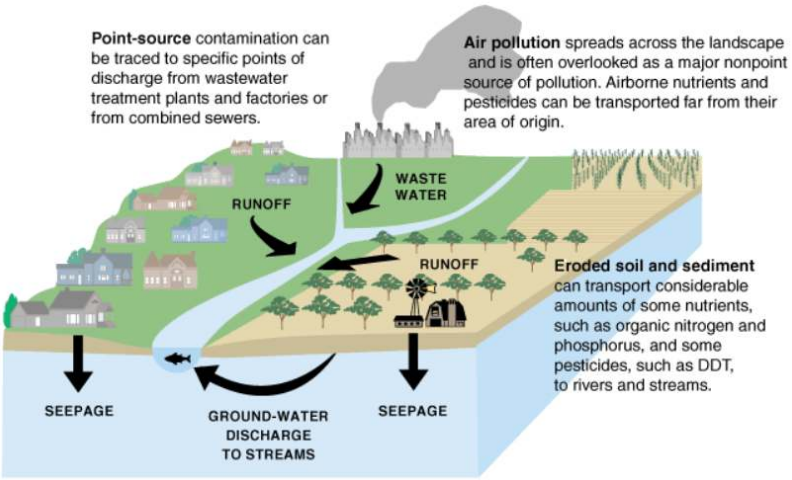


Figure 22.3.5. Sources of Water Contamination. Sources of some water pollutants and movement of pollutants into different water reservoirs of the water cycle. Source: U.S. Geological Survey

Like air pollution, water pollutants may enter the water cycle from point sources, which include identifiable and (generally) relatively small locations, or nonpoint sources, which include large and more diffuse areas. Point sources of pollution include animal factory farms (Figure 22.3.6) that raise a large number and high density of livestock such as cows, pigs, and chickens.



Figure 22.3.6. Large animal farms are often referred to as concentrated feeding operations (CFOs). These farms are considered potential point sources of pollution because untreated animal waste may enter nearby waterbodies as untreated sewage. Credit: ehp.gov

Included in point sources are pipes from factories or sewage treatment plants. Combined sewer systems that have a single set of underground pipes to collect both sewage and stormwater runoff from streets for wastewater treatment can be major point sources of pollutants. During heavy rain, stormwater runoff may exceed sewer capacity, causing it to back up and spilling untreated sewage directly into surface waters (Figure 22.3.7).

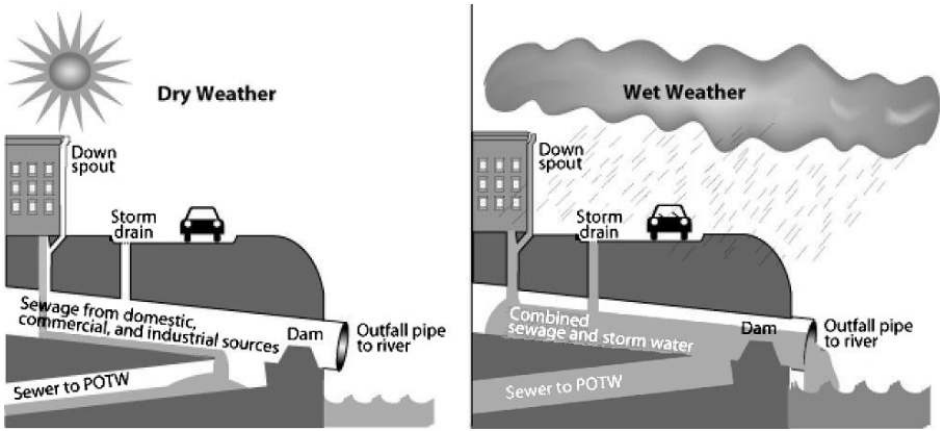


Figure 22.3.7. Combined Sewer System A combined sewer system is a possible major point source of water pollution during heavy rain due to overflow of untreated sewage. During dry weather (and small storms), all flows are handled by the publicly-owned treatment works. During large storms, the relief structure allows some of the combined stormwater and sewage to be discharged untreated to an adjacent water body. Source: U.S. Environmental Protection Agency at Wikimedia Commons

Non-point sources of pollution include agricultural fields, cities, and abandoned mines. Rainfall runs over the land and through the ground, picking up pollutants such as herbicides, pesticides, and fertilizer from agricultural fields and lawns; oil, antifreeze, animal waste, and road salt from urban areas; and acid and toxic elements from abandoned mines. Then, this pollution is carried into surface water bodies and groundwater. Non-point source pollution, which is the leading cause of water pollution, is usually much more difficult and expensive to control than point source pollution because of its low concentration, multiple sources, and much greater volume of water.

Video



In this 9-minute video, discover how the plastic we dump into the ocean might be hiding in plain sight. Question after watching: What is the ultimate solution to plastic waste in the ocean? What part can individuals play in this solution? What part can corporations play?

Population

Humans, while subject to the same ecological constraints as any other species (a need for nutrients, water, etc.), have some features as individuals and some as a population that make them a unique species. Unlike most other organisms, humans have the capacity to alter their number of offspring, level of resource consumption and distribution. While most women around the world could potentially have the same number of children during their lives, the number they actually have is affected by many factors. Depending upon technological, cultural, economic and educational factors, people around the world have families of different sizes. Additionally, unlike other organisms, humans invent and alter technology, which allows them to change their environment. This ability makes it difficult to determine the human carrying capacity (Figure 22.3.8).

For example, families in developing nations are often larger, but less resource-intensive (e.g., they use fewer resources per person) than those in more developed nations. However, increasingly, human populations wish to have a "western" standard of living. An increase in the world's average standard of living significantly lowers the potential human carrying capacity of the earth. Therefore, in order to reduce their impact as a species, humans must not only reduce the resources they use per person, they must also reduce their average family size.

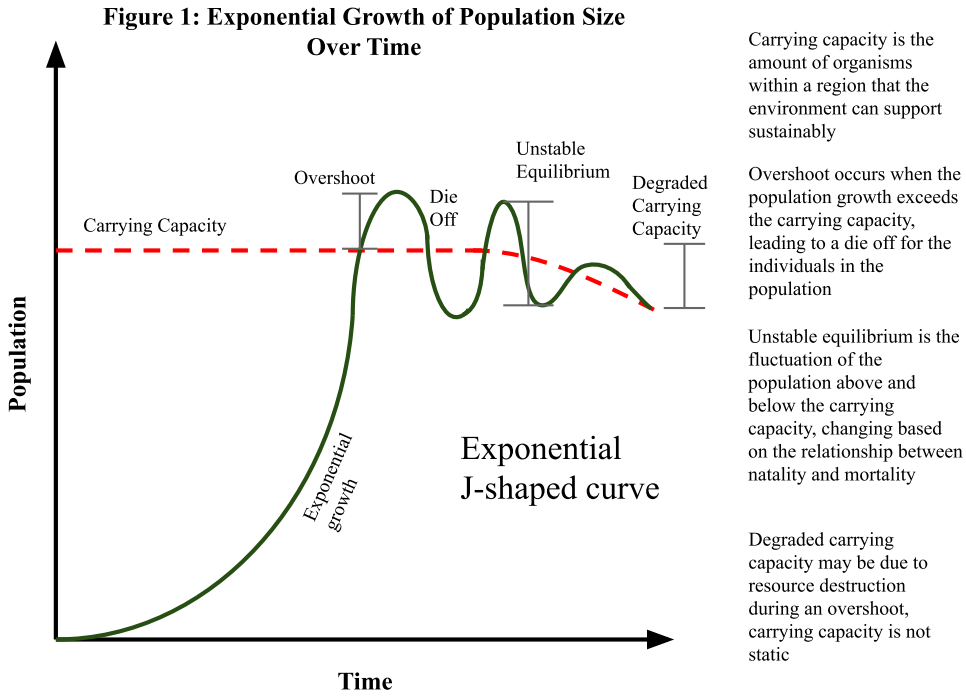


Figure 22.3.8: Reaching carrying capacity through exponential growth, followed by die-off and carrying capacity degradation (Copyright; Nchisick CC BY-SA 4.0)

Human Resource Utilization

Humans have always made an impact on the environment through their use of resources. For example, early humans were primarily hunter-gatherers who used tools to survive. They fashioned wood and stone tools for hunting and food preparation, and used fire for cooking. Early humans developed methods for changing habitats to suit their needs and herding wild animals. As time passed, humans developed more tools and techniques and came to rely on that technology in their daily lives. Although the tools of early humans were primitive by today's standards, they significantly affected the environment and probably hastened the extinction of some large Ice Age mammals.

Over the last 10,000 years, land clearing for agriculture has destroyed and degraded the habitats of many species of plants and animals. Today, growing populations in less developed countries are rapidly clearing tropical forests and savannas for agricultural use. These tropical rainforests and savannas provide habitat for most of the earth's species. It has become clear that modern agricultural practices are not sustainable. Once-fertile areas are becoming infertile because of overgrazing, erosion and nutrient depletion. Furthermore, modern agriculture requires large inputs of energy and fertilizers, usually produced from nonrenewable fossil fuels.

Advanced industrialization leads to many changes in human society, and some of those changes negatively affect the supply of natural resources and result in environmental degradation. These changes include increased production and consumption of goods by humans, dependence on non-renewable resources such as oil and coal, production of synthetic materials (which may be toxic or non-biodegradable), and consumption of large amounts of energy at home and work. For example, if everyone on the planet lived as the average American, humanity would need the equivalent of 7.5 Earths to support everyone.

Other changes may have positive benefits. These include the creation and mass production of useful and affordable products, significant increases in the average **gross national product** per person, large increases in agricultural productivity, sharp rises in average life expectancy, and a gradual decline in population growth rates. The information age was born with the invention of miniaturized electronics such as integrated circuits and computer central processing units. This stage in human development has changed and continues to change society as we know it. By making good use of information technologies, less developed countries may be able to reduce potential environmental problems as their economies expand in the future. With so much information easily

available, developing countries may not repeat the environmental mistakes that more developed countries made as they became industrialized.

Predator Losses

"The loss of apex consumers is arguably humankind's most pervasive influence on the natural world. This is true in part because it has occurred globally and in part because extinctions are by their very nature perpetual, whereas most other environmental impacts are potentially reversible on decadal to millenial time scales. Recent research suggests that the disappearance of these animals reverberates further than previously anticipated, with far-reaching effects on processes as diverse as the dynamics of disease; fire; carbon sequestration; invasive species; and biogeochemical exchanges among Earth's soil, water, and atmosphere."[1] The loss of these predators leads to what is known as **trophic cascades**.

"Predation is ubiquitous in nature and can be an important component of both ecological and evolutionary interactions. One of the most striking features of predators is how often they cause evolutionary diversification in natural systems. Predators are effective agents of natural selection because they possess key traits that allow them to capture and consume their prey; they adopt different strategies to do so, and they are common, but not too common, such that they can drive prey evolution without driving prey species to extinction."[2]

"Classic ecological studies that viewed predators as static entities that interact with prey in fixed ways resulting in predictable population dynamics are likely too simplistic. Today it is recognized that both predator and prey populations evolve—and that this evolution can happen very rapidly, even on ecological time scales, often with more than two species involved."[2]

"Ecosystems may be shaped by the loss of consumers. The loss of a single predator species may reverberate through the community. The loss of apex consumers reduces food chain length, thus altering the intensity of herbivory and the abundance and composition of plants in largely predictable ways. The transitions in ecosystems that characterize such changes are often abrupt, are sometimes difficult to reverse, and commonly lead to radically different patterns and pathways of energy and [matter]."[2]

Video



Scientists have discovered that reintroducing apex predators has led to successful recovery of previously damaged ecosystems, profiled in this 6-minute video from the IUCN.

Question after watching: Why do apex predators play such a crucial role in ecosystems and how can we effectively preserve them?

? Optional Activity 22.3.2

Wolves are a keystone species in Yellowstone National Park, Wyoming, USA. Predict what would happen if they were hunted to extinction.

A. Many species would increase and the elk population would disappear.
B. Many species would disappear and the elk population would initially increase.
C. Many species along with elk population would increase.
D. Many species, along with the elk population, would disappear.

Answer

B. Many species would disappear and the elk population would initially increase.

Overharvesting

Overharvesting is a serious threat to many species, but particularly to aquatic species. There are many examples of regulated fisheries (including hunting of marine mammals and harvesting of crustaceans and other species) monitored by fisheries scientists that have nevertheless collapsed. The western Atlantic cod fishery is the most spectacular recent collapse. While it was a hugely productive fishery for 400 years, the introduction of modern factory trawlers in the 1980s and the pressure on the fishery led to it becoming unsustainable. The causes of fishery collapse are both economic and political in nature.

Most fisheries are managed as a common resource, available to anyone willing to fish, even when the fishing territory lies within a country's territorial waters. Common resources are subject to an economic pressure known as the tragedy of the commons, in which fishers have little motivation to exercise restraint in harvesting a fishery when they do not own the fishery. The general outcome of harvests of resources held in common is their overexploitation. While large fisheries are regulated to attempt to avoid this pressure, it still exists in the background. This overexploitation is exacerbated when access to the fishery is open and unregulated and when technology gives fishers the ability to overfish. In a few fisheries, the biological growth of the resource is less than the potential growth of the profits made from fishing if that time and money were invested elsewhere. In these cases—whales are an example—economic forces will drive toward fishing the population to extinction.

Video



Learn about overfishing and its effects on ecosystems, food security, jobs, economies, and coastal cultures in this 4.5-minute video.

Question after watching: What can communities do to ensure their local waters are fished sustainably?

Coral reefs are extremely diverse marine ecosystems that face peril from several processes. Reefs are home to 1/3 of the world's marine fish species—about 4,000 species—despite making up only one percent of marine habitat. Most home marine aquaria house coral reef species that are wild-caught organisms—not cultured organisms. Although no marine species is known to have been driven extinct by the pet trade, there are studies showing that populations of some species have declined in response to harvesting,

indicating that the harvest is not sustainable at those levels. There are also concerns about the effect of the pet trade on some terrestrial species such as turtles, amphibians, birds, plants, and even the orangutans Figure 22.3.9.



Figure 22.3.9. Harvesting of pangolins for their scales and meat, and as curiosities, has led to a drastic decline in population size for this fascinating creature. *This work by David Brossard is licensed under CC BY 4.0*

Many around the world eat wild animals for food. Hunting is practiced throughout the world, but hunting practices, particularly in equatorial Africa and parts of Asia, are believed to threaten several species with extinction. Traditionally, wild meat in Africa was hunted to feed families directly. However, recent commercialization of the practice now has wild meat available in grocery stores, which has increased harvest rates to the level of unsustainability. Additionally, human population growth has increased the need for protein foods that are not being met from agriculture. Species threatened by the wild meat trade are mostly mammals including many monkeys and the great apes living in the Congo basin.

Climate Change

Climate change, and specifically the anthropogenic (meaning, caused by humans) warming trend presently underway, is recognized as a major extinction threat, particularly when combined with other threats such as habitat loss. Extinction rate estimates range from 15 percent to 40 percent of species committed to extinction by 2050 due to climate change. Climate change will alter regional climates, including rainfall and snowfall patterns, making habitats less hospitable to the species living in them. The warming trend will shift colder climates toward the north and south poles, forcing species to move with their adapted climate norms while facing habitat gaps along the way.

The shifting ranges will impose new competitive regimes on species as they find themselves in contact with other species not present in their historic range. One such unexpected species contact is between polar bears and grizzly bears (Figure 22.3.10). Previously, these two species had separate ranges. Now, their ranges are overlapping and there are documented cases of these two species mating and producing viable offspring. Changing climates also throw off species' delicate timing adaptations to seasonal food resources and breeding times. Many contemporary mismatches to shifts in resource availability and timing have already been documented.



Figure 22.3.10: Since 2008, grizzly bears (*Ursus arctos horribilis*) have been spotted farther north than their historic range, a possible consequence of climate change. As a result, grizzly bear habitat now overlaps polar bear (*Ursus maritimus*) habitat. The two kinds of bears, which are capable of mating and producing viable offspring, are considered separate species as historically they lived in different habitats and never met. However, in 2006 a hunter shot a wild grizzly-polar bear hybrid known as a grolar bear, the first wild hybrid ever found.

Range shifts are already being observed: for example, some European bird species ranges have moved 91 km northward. The same study suggested that the optimal shift based on warming trends was double that distance, suggesting that the populations are not moving quickly enough. Range shifts have also been observed in plants, butterflies, other insects, freshwater fishes, reptiles, and mammals.

Climate gradients will also move up mountains, eventually crowding species higher in altitude and eliminating the habitat for those species adapted to the highest elevations. Some climates will completely disappear. The rate of warming appears to be accelerated in the Arctic, which is recognized as a serious threat to polar bear populations that require sea ice to hunt seals during the winter months: seals are the only source of protein available to polar bears. A trend towards decreasing sea ice coverage has occurred since observations began in the mid-twentieth century. The rate of decline observed in recent years is far greater than previously predicted by climate models.

Finally, climate change will raise ocean levels due to meltwater from glaciers and the greater volume of warmer water. Shorelines will be inundated, reducing island size, which will have an effect on some species, and a number of islands will disappear entirely. Additionally, the gradual melting and subsequent refreezing of the poles, glaciers, and higher-elevation mountains—a cycle that has provided freshwater to environments for centuries—will also be jeopardized. This could result in an overabundance of salt water and a shortage of fresh water.

More on climate change follows in Unit 5.3.

Video



This 6-minute video from PBS discusses that as the world figures out how to live with a rapidly changing climate, traditional knowledge from indigenous cultures could help Western Science understand just how things are transforming.

Question after watching: In what ways is Indigenous Science dynamic regarding climate change? In what areas are Indigenous people facing discrimination in science?

Optional Activity 22.3.3

Converting a prairie to a farm field is an example of _____.

A. overharvesting
B. habitat loss
C. exotic species
D. climate change

Answer

B. habitat loss

Optional Activity 22.3.4

Loss of biodiversity and acceleration of extinction rates have several causes. Which of the following situations causes direct loss of biodiversity owing to overexploitation?

A. fishing cod at a rate that is greater than natural replacement
B. building a housing subdivision in place of second-growth forest
C. introduction of an invasive ornamental plant in a new ecosystem
D. emission of greenhouse gases increasing the average temperatures of an area

Answer

A. fishing cod at a rate that is greater than natural replacement

Video



In this 3.5-minute video, learn of a 2019 United Nations report that says humans are transforming the planet's natural habitat at an unprecedented rate.

Question after watching: Are you optimistic or pessimistic of humans' capability to change and reduce their collective ecological footprint?

Footnotes:

1. Estes, J.A. et al. 2011. Trophic Downgrading of Planet Earth. *Science.* 333(6040): 301-306: https://doi.org/10.1126/science.1205106

2. Johnson, J.B. and M.C. Belk. 2020. Predators as Agents of Selection and Diversification. *Diversity.* 12(11): 415; https://doi.org/10.3390/d12110415

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22.4: Preserving Biodiversity

Preserving Biodiversity

- Please read and watch the following Learning Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 2 hours.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.



Introduction

Preserving biodiversity is an extraordinary challenge that must be met by a greater understanding of biodiversity itself, changes in human behavior and beliefs, and various preservation strategies. The threats to biodiversity have been recognized for some time. Today, the main efforts to preserve biodiversity involve legislative approaches to regulate human and corporate behavior, setting aside protected areas, and habitat restoration. A lofty goal is to protect 50% of the Earth's natural spaces for wildlife known as the Half-Earth Project, as described by the late Dr. E.O. Wilson below. Others, such as David Attenborough and Dr. Sylvia Earle, weigh in on the issue as well.

Videos



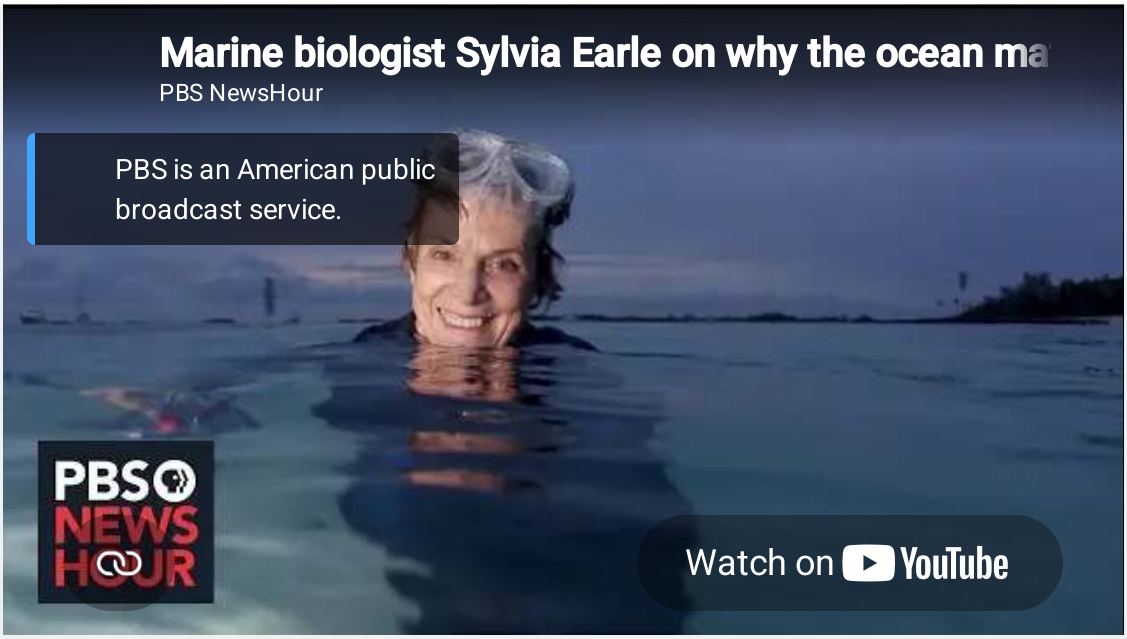


6-minute video with famed conservationist David Attenborough





6-minute video with famed biologist E.O. Wilson





3-minute video with famed marine biologist Sylvia Earle

Question after watching: What common themes do you find in the messages of these conservation ambassadors?

Changing Human Behavior

Ultimately, human behavior will change when human values change. At present, the growing urbanization of the human population is a force that poses challenges to the valuing of biodiversity. Legal avenues can help to protect biodiversity in the meantime.

International Legislation

Legislation throughout the world has been enacted to protect species. The legislation includes international treaties as well as national and provincial laws. The Convention on International Trade in Endangered Species of Wild Fauna and Flora (**CITES**) agreement came into force in 1975. The agreement, and the national legislation that supports it in Canada and most other countries, provides a legal framework for preventing approximately 33,000 listed species from being transported across national borders, thus protecting them from being caught or killed when international trade is involved. The treaty is limited in its reach because it only deals with the international movement of organisms or their parts. It is also limited by some countries' ability or willingness to enforce the treaty and supporting legislation. The illegal trade in organisms and their parts is probably a market in the hundreds of millions of dollars. Illegal wildlife trade is monitored by a non-profit: Trade Records Analysis of Flora and Fauna in Commerce (**TRAFFIC**).

The **Convention on Biological Diversity** is now the leading international treaty to advance the conservation of biodiversity, within the context of a comprehensive agenda for sustainable development. The three key goals of the Convention are the conservation of biodiversity, the sustainable use of its components, and the equitable sharing of benefits from the use of genetic resources. The 194 ratified parties to the Convention are engaged in a multitude of cooperative initiatives and information and technology sharing, and are committed to identify and conserve their biodiversity.

A key action is to periodically undertake science assessments of the status of global biodiversity. Broadly speaking, the most recent assessment found that the prospects of biodiversity were rapidly worsening in many parts of the world, although considerable progress was being made in cooperative planning and in the designation of protected areas and other conservation measures in many countries. It is too soon to tell whether these international actions will be successful because the programs began only in the late 1970s (as an earlier program called the World Conservation Strategy). However, it is encouraging to know that this sort of comprehensive international effort exists and that almost all of Earth's nations are participating, including countries in all stages of economic development.

On an international level, important wilderness lands have been designated by the United Nations through its "**Man and the Biosphere Program**." This program was established in 1973 to protect examples of major natural regions throughout the world, and provide opportunities for ecological research and education.

Biosphere reserves are organized into three interrelated zones: the **core area**, the **buffer zone** and the **transition area**. The core area contains the landscape and ecosystems to be preserved. The buffer zone is an area where activities are controlled to protect the core area. The outer transition area contains a variety of agricultural activities, human settlements and other uses. Local communities, conservation agencies, scientists and private enterprises that have a stake in the management of the region work together to make the reserves work. Mt Kenya in Africa and the Galapagos Islands are examples of wilderness areas protected under this provision.





Optional Activity 22.4.1

The Convention on International Trade in Endangered Species (CITES) passed a resolution to protect rhinoceroses in the wild. Rhinoceroses have been hunted to the brink of extinction because their horns, which are made of the protein keratin, the same as humans' fingernails and hair, are considered an aphrodisiac and a powerful drug in some cultures. Why does the protection of rhinoceroses require an international agreement?

A. The rhinoceroses are hunted in their native countries, but the trade crosses borders.
B. The use of rhinoceros' horns as an aphrodisiac has showed negative effects internationally.
C. The hunters from different countries travel to the native country to hunt for rhinoceroses.
D. Their demand is greater in foreign countries as compared to their native countries.

Answer

A. The rhinoceroses are hunted in their native countries, but the trade crosses borders.

US Legislation

Within many countries there are laws that protect endangered species and that regulate hunting and fishing. In the United States, the **Endangered Species Act** (ESA) was enacted in 1973. When an at-risk species is listed by the Act, the U.S. Fish & Wildlife Service is required by law to develop a management plan to protect the species and bring it back to sustainable numbers. The ESA, and others like it in other countries, is a useful tool, but it suffers because it is often difficult to get a species listed or to get an effective management plan in place once a species is listed.

The **Migratory Bird Treaty Act** (MBTA) is an agreement between the United States and Canada that was signed into law in 1918 in response to declines in North American bird species caused by hunting. The Act now lists over 800 protected species. It makes it illegal to disturb or kill the protected species or distribute their parts (much of the hunting of birds in the past was for their feathers). Examples of protected species include northern cardinals, the red-tailed hawk, and the American black vulture.

The ESA recognizes five categories of risk, each of which has a specific meaning in terms of imminent threats to the future survival of the species (COSEWIC, 2015).

- **Extinct** refers to any species of wildlife that was formerly indigenous to the US but no longer exists anywhere in the world.
- **Extirpated** refers to any species or subspecies that was formerly indigenous to the US but now only survives in the captivity or elsewhere, usually in Canada or Mexico.
- **Endangered** refers to native species that are faced with imminent extinction or extirpation throughout all or a significant portion of their range.
- **Threatened** refers to any indigenous taxon that is likely to become critically imperiled unless factors affecting its status are reversed.
- **Vulnerable** refers to any indigenous species that is not currently imperiled but is at risk of becoming so because of small or declining numbers, occurrence at the fringe of its range or in restricted areas, habitat fragmentation, or some other reason.

It must be recognized that the designation of species at risk is a continuing and always incomplete process. For instance, because the conservation status of only a few species of invertebrates has been investigated, critically imperiled species in this group are enormously under-represented in the ESA list. Unfortunately, more rapid progress is constrained by a shortage of funding for research and monitoring of endangered species, and by a lack of specialists with the necessary taxonomic and ecological skills and knowledge.

Of course, it is not sufficient merely to designate species as being at risk of extirpation or extinction. If their status is to be improved, the species and their habitats must also be protected. Remarkably, the US federal government has not yet enacted effective legislation to protect endangered species and their habitat across the whole of the country. However, this situation is starting to change.

However, federal legislation has little direct influence on the status of the many threatened and vulnerable that are living on state, private, or Indigenous land. Most importantly, the Act does not fully address the protection of habitat of critically imperiled species off federal land. To some degree, this deficiency is covered by legislation that has been enacted by states. However, their legislations are also not very effective, because they, too, do not protect the habitat of species at risk, especially on private land. Such a piecemeal approach results in uneven levels of protection for species-at-risk, which is unacceptable from the conservation viewpoint.

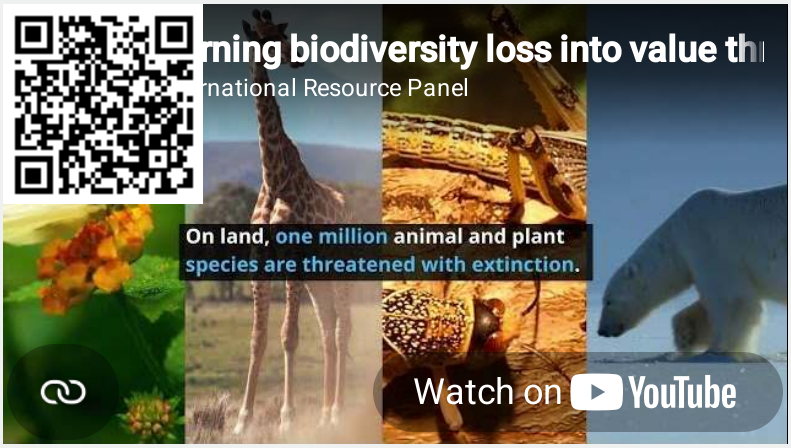
The lack of effective protection of species-at-risk in US is raising controversy. Governments feel the need to demonstrate that they are making rapid progress toward sustainability, an important component of which involves the protection of native species and their habitats. Unfortunately, the progress to date has been lacking and is not yet effective in protecting our biodiversity most at-risk. Hopefully, the lobbying efforts of non-governmental organizations (NGOs) will result in appropriate changes to the currently weak legislation of all levels of government.

Most of the natural ecosystems of the United States now exist only as small remnants of their former extent. Because of this, they are as endangered as the species they support. The most endangered of our natural ecosystems are:

- the tall-grass prairie of the Midwest
- old-growth forests of all of the US
- dry coastal forests of the southeast
- deserts of the southwest
- most freshwater wetlands

Some of these ecosystems are also rich in endangered species. It is imperative that the remaining areas of these endangered ecosystems become preserved in parks and other kinds of protected areas.

Video



In this 3 min video, you will be introduced to the argument that biodiversity loss results in economic loss in diverse ways, therefore natural resource management practices need to be applied.

Question after watching: Do you agree that biodiversity loss should be treated with natural resource management practices? What are the advantages and disadvantages of doing this?

Indigenous Connections: Preserving Salmon Fisheries

"Pacific salmon—fish known by a host of Indigenous names throughout their vast geographic range (genus Oncorhynchus)—have been in a state of decline in British Columbia (BC), Canada for several decades (Price et al. 2017) such that a growing number of wild salmon populations have been assessed as “at risk”’ (from Special Concern (n = 5 populations) to Threatened (n = 3) to Endangered (n = 10)) by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC; Government of Canada 2018). As both ecological and cultural keystone species, without the continued existence of salmon, ecosystems and societies alike would be entirely transformed (Willson and Halupka 1995; Garibaldi and Turner 2004)."[1]

"For the Nisga’a, which sits on the BC–Alaska border (and to which the lead author belongs), salmon are vital. They shape *ayuukhl* (code of law) and *adaawak* (oral histories), they figure centrally in *yukw* (feasts, known externally as “potlatches”), and they are a focal point of the Nisga’a Treaty (2000) that defines Nisga’a rights tied specifically to salmon. As Nisga’a and indeed many Indigenous nations identify as “Salmon People” (Columbia River Inter-Tribal Fish Commission 2020; Earth Economics 2021), there is serious concern about what will become of salmon-linked cultures, economies, knowledges, languages, laws, well-being, and worldviews as the annual return of these anadromous fish to rivers across the Pacific Northwest become increasingly unpredictable and, in many systems, Indigenous fisheries for wild salmon become a shadow of their former selves (Jacob, McDaniels and Hinch 2010; Atlas et al. 2021). Decolonial research strategies that respect Indigenous intellectual traditions and affirm Indigenous control over Indigenous knowledge are critical to the maintenance and recovery of salmon-based knowledge systems and salmon populations (Simpson 2004; Bingham et al. 2021)."[1]

> *Not only would it behoove fisheries scientists to use all and the best tools and knowledge available at this time of [social-ecological] crisis, irrespective of their origin and the perceived objectivity and superiority of Western scientific approaches, but this would importantly serve decolonial and reconciliatory efforts that help rectify uneven power relations, knowledge inequalities, and other racially linked and unjust dynamics in fisheries.*[3]

"Indigenous peoples have been managing landscapes more or less sustainably for thousands of years. Indigenous peoples’ successes stem, in part, from the fact that many Indigenous worldviews recognize that species do not exist in isolation; they are part of a natural system."[2]

"TEK provides invaluable time-tested resource management practices that can be used alongside WS to develop more workable and effective approaches to current resource management strategies than either could accomplish alone. In fact, it has become a policy requirement in Canada, and in particular Northern Canada, that TEK be incorporated into environmental assessments affecting wildlife management including: migratory birds, species at risk, forest practices, and fisheries management (Usher, 2000)."3

The Nisga'a Nation's understanding of, and work with, Pacific salmon is an excellent example of the role that Indigenous Science plays in understanding biodiversity and how to protect species and habitat in a sustainable manner.

"Through partnerships with 18 communities of “Salmon People” and semi-structured interviews with 48 knowledge holders (i.e., Elders), we learned that, on average, Elders spent more than half of a century actively engaged in salmon fishing and processing. Modern salmon catches are reported to be approximately one-sixth of what they were estimated to be five to seven decades ago, and the top five threats to salmon identified by Elders included (i) aquaculture, (ii) climate change, (iii) contaminants, (iv) industrial development, and (v) infectious diseases. Threat priorities varied regionally, reflecting distinct lived experiences and regional variation in the prevalence and impact of different threats. Elders perceived threats to salmon equally as threats to aquatic health and human well-being, with evidence that the relationships between people and water, and salmon and people, are being profoundly transformed."[1]

"The Nisga'a people of northern British Columbia live in the Nass Valley near Alaska. Every spring, members of some Nisga'a families still walk their salmon streams to ensure that spawning channels are clear of debris and that salmon are not obstructed in their ascent to spawning grounds. Concerned with the multiple perils faced by their Nass River salmon, the Nisga'a have themselves implemented a salmon protection project that uses both the ancient technology and wisdom practices, as well as modern statistical methods of data analysis to provide more reliable fish counts than electronic tracking systems (Figure 22.4.1). The Nisga'a project, which earned a Department of Fisheries and Oceans Canada award, is described in the following account by Corsiglia and Snively (1997)

> *"Observing that electronic fish counters can be inaccurate, the Nisga'a have instituted an ingenious fish counting system in the Nass River that combines ancient fish wheel technology with modern statistical methods. The ancient fish wheel was made of cedar wood and nettle fibre mesh, and the elongated axle of the fish wheel was fitted with three parallel vanes constructed in the form of large, flattened dip nets. The swift moving downstream current turned the wheel by exerting force against the submerged vanes, and as the companion vanes rose in turn, they gently caught and uplifted the fish as they swam upriver. As each vane rose from the horizontal, the fish slid toward wooden baffles that guided them out of the side of the fish wheel and into submerged holding baskets. This technology provided the Nisga'a with an effortless fishing technique as well as a ready supply of fresh salmon."*[3] *(p. 19)*

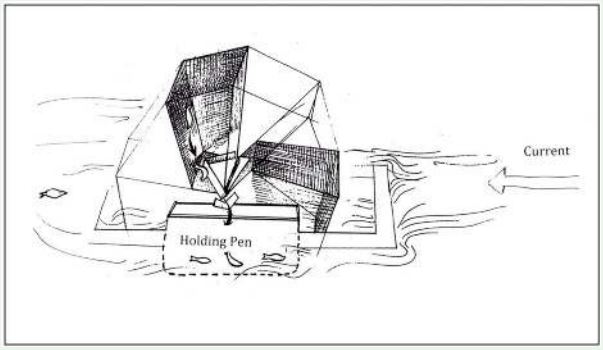


Figure 22.4.1. *Nisga'a fish wheel showing holding pen. Illustration by Laura Corsiglia (1997).*

"Modern Nisga'a fishing wheels are made of aircraft aluminum and nylon mesh. Like their predecessors, these fish wheels allow fish to be captured live and held in holding tanks. This enables the Nisga'a to tag and count the fish by means of statistical analysis. Returning salmon are first caught using a fish wheel at a lower river station where fish are tagged. Fish are also caught at an upper fish station where the proportion of tagged fish is used to calculate returns. Reportedly, "this system provides more accurate and reliable data than that collected by electronic tracking systems alone" (Chief Harry Nyce, personal communication to John Corsiglia, 1986)."[3]

In a similar context, the Wuikinuxv of central British Columbia identify the season's quotas for salmon not only with humans in mind but also with bears. They recognize that not only are the bears an important part of their ecosystem and culture but, if the bears are well-fed with salmon, they are less likely to seek out food in areas where humans live. The forest and other inhabitants that the Wuikinuxv rely on are nourished in one way or another by the remains of the salmon.[2]

"The Wuikinuxv calculate fishing quotas based on salmon availability and existing bear density, assuming that, as salmon populations recover, the bear population will grow until it is limited by some other factor. Salmon and bear numbers are then balanced against the benefits of salmon to human fishers. Spawning targets aim to balance the costs felt by humans and bears, the latter of which encompasses the needs of other beings in the ecosystem. In contrast, Canada manages salmon at the federal level, while bears are managed provincially, making holistic management difficult. The smaller, more intimate scale of Indigenous management efforts, in contrast, allows closer observation of the landscape...and demonstrates how local knowledge is often undervalued".[2]

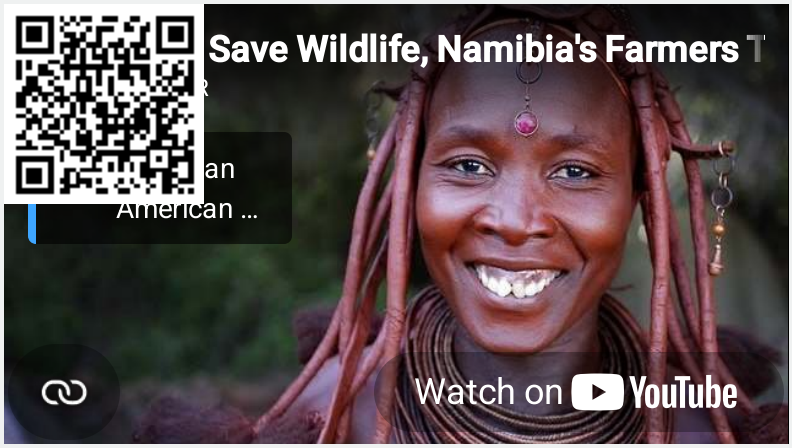
"In a decolonized approach to conservation, the observations of people living in the area would be given proper respect, and systems would be in place to incorporate those observations into models. Another step toward decolonizing conservation...is for settler governments to work with Indigenous communities as equals rather than as just one of many stakeholders. Resource stewardship should be inseparable from Indigenous sovereignty, assert the study's authors."[2]



In this 2.5-minute video, you will meet Kasey Stirling, a Nlaka'pamux, Mi'kmaq, and Acadienne researcher, is a master's student in the Centre for Indigenous Fisheries at the Institute for the Oceans and Fisheries (IOF). Stirling works in partnership with the First Nations Fisheries Legacy Fund, a collective of six Lower Fraser First Nations (Katzie, Kwantlen, Kwikwetlem, Musqueam, Tsleil-Waututh, and Tsawwassen), to co-develop a more culturally relevant framework for watershed health assessment, which directly impacts salmon populations.

Question after watching: What might be gained from scientists working in partnership with Indigenous communities to preserve diversity? What type of knowledge and perspective can each group bring to the partnership?

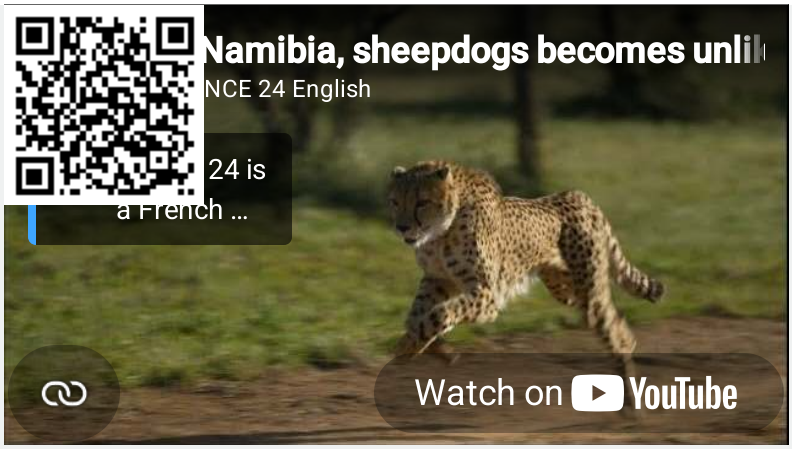
Video



Imagine the U.S. government told people who live around Yellowstone, say, all those bears and wolves are now yours to take care of, and for doing that you get to keep the money from tourists who come to see those animals. It can sound radical, but that's essentially what the government of Namibia is doing right now. And as a result, wildlife numbers are rising there - unlike much of Africa.
Question after watching:

Video

https://bio.libretexts.org/@go/page/118174



Namibia is home to around 3,500 cheetahs, or half the world's cheetah population. But the animals there are threatened by farmers, who often shoot them on sight to defend their herds. To protect the big cats, one wildlife sanctuary had the idea of training sheepdogs.

Question after watching:

Adapting to and Mitigating Climate Change

More on climate change was discussed in Unit 6, but it should be clear to anyone that climate change has the potential to greatly restructure the world's ecosystems, ecosystem services, and national economies. Many coastal areas will experience rising sea levels and increased flooding, while inland areas may experience desertification and less favorable growing conditions for crops. Poorer countries and communities will suffer the consequences disproportionately because of their limited mobility, high dependence on ecosystem services, and general lack of disaster management infrastructure.

If we are to mitigate the far-reaching impacts of climate change, we must carefully monitor and study changes in biological communities and ecosystem functioning, and how they relate to changes in climate and other stressors. While we may lose some species in a warmer world, we can also prevent many extinctions with proactive wildlife management. It is likely that many existing protected areas will no longer preserve some of the rare and threatened species that currently live in them, necessitating careful planning when establishing new protected areas. Even if climate change is not as severe as predicted, the steps we take now to safeguard biodiversity can only help in the future.

The widespread and dramatic impacts of climate change rightfully deserve much attention. But it is also important to remember that we continue to destroy habitats at a massive scale and increasing pace and this loss of habitat is currently the main cause of species extinctions. The highest priorities for conservation must continue to be the preservation of healthy, intact, and connected ecosystems, and the restoration of degraded ecosystems. These actions will simultaneously reduce the impacts of climate change, by reducing carbon emissions, increasing carbon sequestration, and giving wildlife more opportunities to adjust their ranges, in their own time, as the world's climate changes.

Videos

https://bio.libretexts.org/@go/page/118174



Indigenous communities in British Columbia are preparing for climate change, as detailed in this 5-minute video. Question after watching: How are Indigenous communities reconnecting to the land in a changing climate? What other strategies are they utilizing internally and sharing with non-Indigenous communities?

Conservation in Preserves

Video



This 10-minute video by Hank Green provides an overview of both conservation science and restoration efforts, described in further detail below.
Question after watching: What conserved spaces are nearest to you? Do you visit them? Do you know of any restoration efforts near where you live?

The establishment of wildlife and ecosystem **preserves** is one of the key tools in conservation efforts (Figure 22.4.2). A preserve is an area of land set aside with varying degrees of protection for the organisms that exist within the boundaries of the preserve. Preserves can be effective in the short term for protecting both species and ecosystems, but they face challenges that scientists are still exploring to strengthen their viability as long-term solutions. Human behavior can still be problematic in these areas as well. For example, the public's misbehavior at national parks has become an increasing problem for governments in many countries.



Figure 22.4.2: National parks, such as Kootenay National Park in British Columbia, help conserve biodiversity. (Parks Canada)

Video

https://bio.libretexts.org/@go/page/118174



This 3-minute video from the National Resources Defense Council profiles the importance of Canada's boreal forest and current threats to this ecosystem.
Question after watching: What strategies might be used to preserve these habitats?

US Preservation

An important human-centered benefit of undeveloped land is their recreational value. Every year, millions of people visit recreational lands such as parks and wilderness areas to experience attractions of the great outdoors: hiking among the giant sequoias in California, traveling on a photo safari in Kenya or just picnicking at a local county park. Besides providing people with obvious health benefits and aesthetic pleasures, recreational lands also generate considerable tourist money for government and local economies.

The United States has set aside more land for public recreational use than any other country. Several different federal organizations provide lands for recreational use: the National Forest System, the U.S. Fish and Wildlife Service, the National Park System and the National Wilderness Preservation System. The National Forest System manages more than 170 forestlands and grasslands, which are available for activities such as camping, fishing, hiking and hunting.

The U.S. Fish and Wildlife Service manage more than 500 National Wildlife Refuges, which not only protect animal habitats and breeding areas but also provide recreational facilities. The National Park System manages more than 380 parks, recreation areas, seashores, trails, monuments, memorials, battlefields and other historic sites. The National Wilderness Preservation System manages more than 630 roadless areas through the aforementioned government services as well as through the Bureau of Land Management.

The **National Park System** consists of more than 80 million acres nationwide. The largest national park is Wrangell-St. Elias National Park and Preserve in Alaska with over 13 million acres. California has eight national parks: Channel Islands, Death Valley, Joshua Tree, Lassen, Redwood, Sequoia, Kings Canyon and Yosemite. Many national parks such as Yosemite, Yellowstone and the Grand Canyon are such popular recreation destinations that the ecosystems of those parks are being severely tested by human activities.

In addition to their primary goal of conserving biodiversity, most parks serve additional purposes, including the support of economically important outdoor recreation and tourism. To some degree, the use of parks for these purposes is a challenge to their ability to function as ecological reserves. For example, strictly interpreted, the ecological values of national parks are not compatible with consumptive uses of their natural resources (such as sport fishing) or with the development of infrastructure to support recreation and tourism (such as campgrounds, golf courses, hotels, roads, ski facilities, and even interpretation facilities).


Here's How the National Park Service Got Started
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HISTORY


Who owns the "wilderness"? - Elyse Cox
TED-Ed
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Every state has also set aside significant amounts of land for recreational use. The California State Park System manages more than one million acres of parklands including: coastal wetlands, estuaries, scenic coastlines, lakes, mountains and desert areas. California's largest state park is Anza-Borrego Desert State Park, which is the largest state park in the United States with 600,000 acres. The stated mission of the California State Park System is: "To provide for the health, inspiration and education of the people of California by helping to preserve the state's extraordinary biological diversity, protecting its most valued natural and cultural resources and creating opportunities for high-quality outdoor recreation."

This is the basic goal of all recreational lands: to manage and conserve natural ecosystems, while supporting a sustainable and balanced level of human use of those areas. Unfortunately, it is a goal which is sometimes difficult to achieve due to the increasing popularity and use of recreational lands.

The "**Wilderness Act of 1964**" created the world's first wilderness system in the United States. Presently, the **National Wilderness Preservation System** contains more than 100 million acres of land that will forever remain wild. A wide range of recreation, scientific and outdoor activities are available in wilderness lands. Mining operations and livestock grazing are permitted to continue in certain wilderness areas where such operations existed prior to an area's designation. Hunting and fishing are also allowed in wilderness areas (except in national parks).

For most people, wilderness lands provide a means for various forms of recreation: hiking, horseback riding, bird watching, fishing, and hunting. People can escape the stress of modern-day life and enjoy an undisturbed look at nature. Wilderness lands provide an essential habitat for a wide array of fish, wildlife, and plants, and are particularly important in protecting endangered species. For scientists, wilderness lands serve as natural laboratories, where studies can be performed that would not be possible in developed areas.

Several other types of public lands complement the designated wilderness land system. These include: national forest roadless areas, national trails system, natural research areas and state and private wilderness lands. The national forest roadless areas consist of millions of acres of wild, undeveloped land without roads that exist on National Forest land outside of designated wilderness lands.

The "**National Trail System**," established by Congress in 1968, includes trails in wilderness areas and other public lands. **Research Natural Areas** located throughout the country on public lands serve as outdoor laboratories to study natural systems. They are intended in part to serve as gene pools for rare and endangered species and as examples of significant natural ecosystems. Some wilderness lands are maintained by states or private organizations. For example, the state of New York has long preserved a region of the Adirondacks as wilderness.

In addition to their primary goal of conserving biodiversity, most parks serve additional purposes, including the support of economically important outdoor recreation and tourism. To some degree, the use of parks for these purposes is a challenge to their ability to function as ecological reserves. For example, strictly interpreted, the ecological values of national parks are not compatible with consumptive uses of their natural resources (such as sport fishing) or with the development of infrastructure to support recreation and tourism (such as campgrounds, golf courses, hotels, roads, ski facilities, and even interpretation facilities).

The ecological-reserve function of many protected areas is also threatened by land-use and management activities that are occurring in their surrounding area. Usually, the most important of the “external” stressors are associated with agriculture, forestry, mining, tourism, or hydroelectric development. In fact, all of the national parks in more southern regions of Canada are significantly threatened in this way.

Banff National Park in southwestern Alberta was the first national park to be established in Canada, in 1885. The original intent was to protect extremely scenic views and hot springs and to develop the area in support of the economic benefits of tourism. It was not until several decades later that the philosophical underpinning of national parks shifted toward the protection of natural values. In any event, the early development of Banff featured the enthusiastic construction of large hotels, golf courses, skiing facilities, major highways, a transcontinental railroad, several villages, and other structures. This pattern continues today with much ongoing construction, coupled with rapid development of the area east of the park for tourism, residential neighborhoods, forestry, and other uses. These facilities severely threaten the long-term viability of the natural values of Banff.

Provincial and territorial governments also have a responsibility to protect natural values within their jurisdiction. These governments have designated many ecological reserves and wilderness areas, supplemented by natural areas that are protected in provincial parks and conservation areas, which are also well-used for recreation. Some municipalities also have natural-area parks that provide habitat for native species. An outstanding example is the city of Windsor, Ontario, which is protecting important remnants of tall-grass prairie and Carolinian forest, and their many species-at-risk.

How Much Area to Preserve?

Due to the way protected lands are allocated (they tend to contain less economically valuable resources rather than being set aside specifically for the species or ecosystems at risk) and the way biodiversity is distributed, determining a target percentage of land or marine habitat that should be protected to maintain biodiversity levels is challenging. The IUCN World Parks Congress estimated that 11.5% of Earth’s land surface was covered by preserves of various kinds in 2003. This area is greater than previous goals; however, it only represents 9 out of 14 recognized major biomes. Research has shown that 12% of all species live only outside preserves; these percentages are much higher when only threatened species and high-quality preserves are considered. For example, high-quality preserves include only about 50% of threatened amphibian species. The conclusion must be that either the percentage of area protected must increase, the percentage of high-quality preserves must increase, or preserves must be targeted with greater attention to biodiversity protection. Researchers argue that more attention to the latter solution is required.

A **biodiversity hotspot** is a conservation concept developed by Norman Myers in 1988. Hotspots are geographical areas that contain high numbers of endemic species. The purpose of the concept was to identify important locations on the planet for conservation efforts, a kind of conservation triage. Protecting hotspots would be able to protect a larger number of species. The original criteria for a hotspot included the presence of 1,500 or more species of endemic plants and 70 percent of the area disturbed by human activity. While many have still not been conserved, there are now 34 identified global biodiversity hotspots (Figure 22.4.3) that contain large numbers of endemic species, which include half of Earth’s endemic plants. In addition to natural spaces, there are numerous human cultural sites preserved in the **UNESCO World Heritage Sites** list: https://whc.unesco.org/en/list/

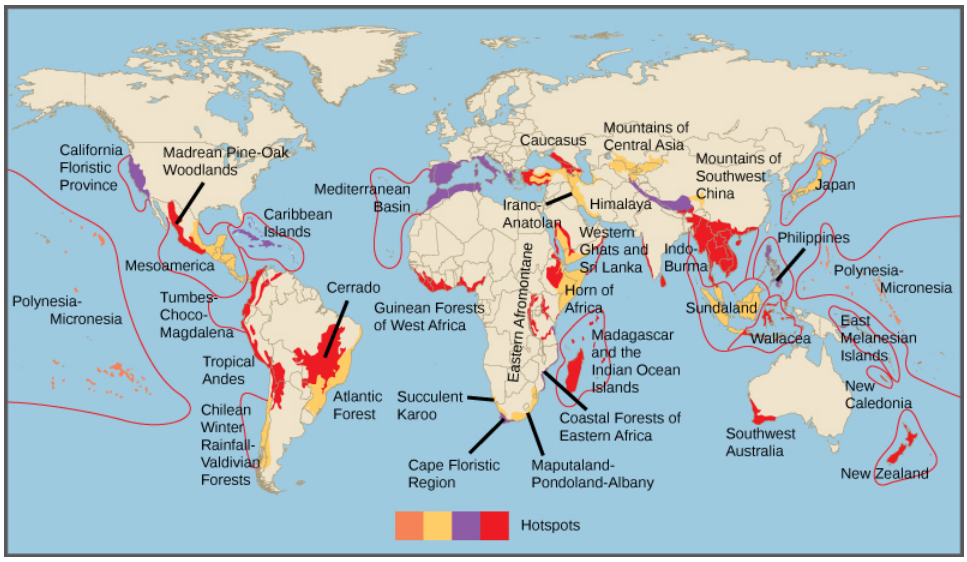


Figure 22.4.3. Conservation International has identified 34 biodiversity hotspots. Although these cover only 2.3 percent of the Earth's surface, 42 percent of the terrestrial vertebrate species and 50 percent of the world's plants are endemic to those hotspots.

? Optional Activity 22.4.2

Scientists are evaluating an island ecosystem for consideration as a biodiversity hotspot. What information should they collect and evaluate as part of their fieldwork to produce their final assessment?

a. the total number of endemic species in an ecosystem
b. the total number of organisms in an ecosystem
c. the total number of species divided by the area of the ecosystem
d. the total number of endangered species in an ecosystem

Answer

A. the total number of endemic species in an ecosystem.

Preserve Design

There has been extensive research into optimal preserve designs for maintaining biodiversity. The fundamental principle behind much of the research has been the seminal theoretical work of Robert H. MacArthur and Edward O. Wilson published in 1967 on island biogeography.[1] This work sought to understand the factors affecting biodiversity on islands. The fundamental conclusion was that biodiversity on an island was a function of the origin of species through migration, speciation, and extinction on that island. Islands farther from the mainland are harder to get to, so migration is lower and the equilibrium number of species is lower. Within island populations, evidence suggests that the number of species gradually increases to a level similar to the numbers on the mainland from which the species is suspected to have migrated. In addition, smaller islands are harder to find, so their immigration rates for new species are lower. Smaller islands are also less geographically diverse so there are fewer niches to promote speciation. And finally, smaller islands support smaller populations, so the probability of extinction is higher.

As islands get larger, the number of species accelerates, although the effect of island area on species numbers is not a direct correlation. Conservation preserves can be seen as "islands" of habitat within "an ocean" of non-habitat. For a species to persist in a preserve, the preserve must be large enough. The critical size depends, in part, on the home range that is characteristic of the species. A preserve for wolves, which ranges hundreds of kilometers, must be much larger than a preserve for butterflies, which might range within ten kilometers during its lifetime. But larger preserves have more core area of optimal habitat for individual species, they have more niches to support more species, and they attract more species because they can be found and reached more easily.

Preserves perform better when there are buffer zones around them of suboptimal habitat. The buffer allows organisms to exit the boundaries of the preserve without immediate negative consequences from predation or lack of resources. One large preserve is

better than the same area of several smaller preserves because there is more core habitat unaffected by edges. For this same reason, preserves in the shape of a square or circle will be better than a preserve with many thin "arms." If preserves must be smaller, then providing wildlife corridors between them so that individuals and their genes can move between the preserves, for example along rivers and streams, will make the smaller preserves behave more like one large one. All of these factors are taken into consideration when planning the nature of a preserve before the land is set aside.

In addition to the physical, biological, and ecological specifications of a preserve, there are a variety of policy, legislative, and enforcement specifications related to the uses of the preserve for functions other than the protection of species. These can include anything from timber extraction, mineral extraction, regulated hunting, human habitation, and non-destructive human recreation. Many of these policy decisions are made based on political pressures rather than conservation considerations. In some cases, wildlife protection policies have been so strict that subsistence-living Indigenous populations have been forced from ancestral lands that fell within a preserve. In other cases, even if a preserve is designed to protect wildlife, if the protections are not or cannot be enforced, the preserve status will have little meaning in the face of illegal poaching and timber extraction. This is a widespread problem with preserves in areas of the tropics.

? Optional Activity 22.4.3

A preserve design is proposed for a densely populated suburban area. Which overall design plan would be best for preservation of local ecosystems?

A. Set up many, small, unconnected, protected areas.
B. Select one, small area that is isolated from residences.
C. Plan buffer zones around all backyard spaces.
D. Set up several, connected, larger areas to be set aside for natural ecosystems.

Answer

D. Set up several, connected, larger areas to be set aside for natural ecosystems.

Limitations on Preserves

Some of the limitations of preserves as conservation tools are evident from the discussion of preserve design. Political and economic pressures typically make preserves smaller, never larger, so setting aside areas that are large enough is difficult. If the area set aside is sufficiently large, there may not be sufficient area to create a buffer around the preserve. In this case, an area on the outer edges of the preserve inevitably becomes a riskier suboptimal habitat for the species in the preserve. Enforcement of protections is also a significant issue in countries without the resources or political will to prevent poaching and illegal resource extraction.

Climate change will create inevitable problems with the location of preserves. The species within them will migrate to higher latitudes as the habitat of the preserve becomes less favorable. Scientists are planning for the effects of global warming on future preserves and striving to predict the need for new preserves to accommodate anticipated changes to habitats; however, the end effectiveness is tenuous since these efforts are prediction-based.

Finally, an argument can be made that conservation preserves reinforce the cultural perception that humans are separate from nature, can exist outside of it, and can only operate in ways that do damage to biodiversity. Creating preserves reduces the pressure on human activities outside the preserves to be sustainable and non-damaging to biodiversity. Ultimately, the political, economic, and human demographic pressures will degrade and reduce the size of conservation preserves if the activities outside them are not altered to be less damaging to biodiversity.

Habitat Restoration

Habitat restoration holds considerable promise as a mechanism for restoring and maintaining biodiversity. Of course, once a species has become extinct, its restoration is impossible. However, **restoration** can improve the biodiversity of degraded ecosystems. Reintroducing wolves, a top predator, to Yellowstone National Park in 1995 led to dramatic changes in the ecosystem that increased biodiversity (Figure 22.4.4).

22.5: Measuring Biodiveristy

Diversity Indices

A **diversity index** is a quantitative measure that reflects how many different types (such as species) there are in a dataset (a community). These indices are statistical representations of biodiversity in different aspects (richness, evenness, and dominance). When diversity indices are used in ecology, the types of interest are usually species, but they can also be other categories, such as genera, families, functional types, or haplotypes. The entities of interest are usually individual plants or animals, and the measure of abundance can be, for example, number of individuals, biomass or coverage.

Richness simply quantifies how many different types the dataset of interest contains. For example, species richness (usually noted *S*) of a dataset is the number of species in the corresponding species list. Richness is a simple measure, so it has been a popular diversity index in ecology, where abundance data are often not available for the datasets of interest.

Although species richness (denoted ***S***) is often used as a measure of biodiversity, of more interest to ecologists and conservation biologists are diversity indices that include both species richness *and* measures of abundance. This is because richness alone does not account for evenness across species. In example 22.2.1 below, both lakes have the same richness, but Lake B is more diverse because abundance is spread more evenly across the species present.

Many different indices of diversity are used by scientists, but below we cover the most widely used.

Simpson's Index

Simpson (1949) developed an index of diversity which is a measure of probability--the less diversity, the greater the probability that two randomly selected individuals will be the same species. In the absence of diversity (1 species), the probability that two individuals randomly selected will be the same is 1. Simpson's Index is calculated as follows:

$$D = \sum_{i=1}^{S} \left(\frac{n_i}{N} \right)^2 \qquad (22.5.1)$$

where n_i is the number of individuals in species *i*, N = total number of individuals of all species, and $n_i/N = p_i$ (proportion of individuals of species i), and *S* = species richness.

The value of Simpson's ***D*** ranges from 0 to 1, with 0 representing infinite diversity and 1 representing no diversity, so the larger the value of ***D***, the lower the diversity. For this reason, Simpson's index is often as its complement (1-***D***). **Simpson's Dominance Index** is the inverse of the Simpson's Index (1/***D***).

Shannon-Weiner Index

Another widely used index of diversity that also considers both species richness and evenness is the Shannon-Weiner Diversity Index, originally proposed by Claude Shannon in 1948. It is also known as **Shannon's diversity index.** The index is related to the concept of uncertainty. If for example, a community has very low diversity, we can be fairly certain of the identity of an organism we might choose by random (high certainty or low uncertainty). If a community is highly diverse and we choose an organism by random, we have a greater uncertainty of which species we will choose (low certainty or high uncertainty).

$$H = -\sum_{i=1}^{S} p_i * \ln p_i \qquad (22.5.2)$$

where p_i = proportion of individuals of species *i*, and ln is the natural logarithm, and *S* = species richness.

The value of ***H*** ranges from 0 to $H_{max.}$ H_{max} is different for each community and depends on species richness. (Note: Shannon-Weiner is often denoted H').

Evenness Index

Species evenness refers to how close in numbers each species in an environment is. So if there are 40 foxes and 1000 dogs, the community is not very even. But if there are 40 foxes and 42 dogs, the community is quite even. The evenness of a community can be represented by Pielou's evenness index (Pielou 1966):

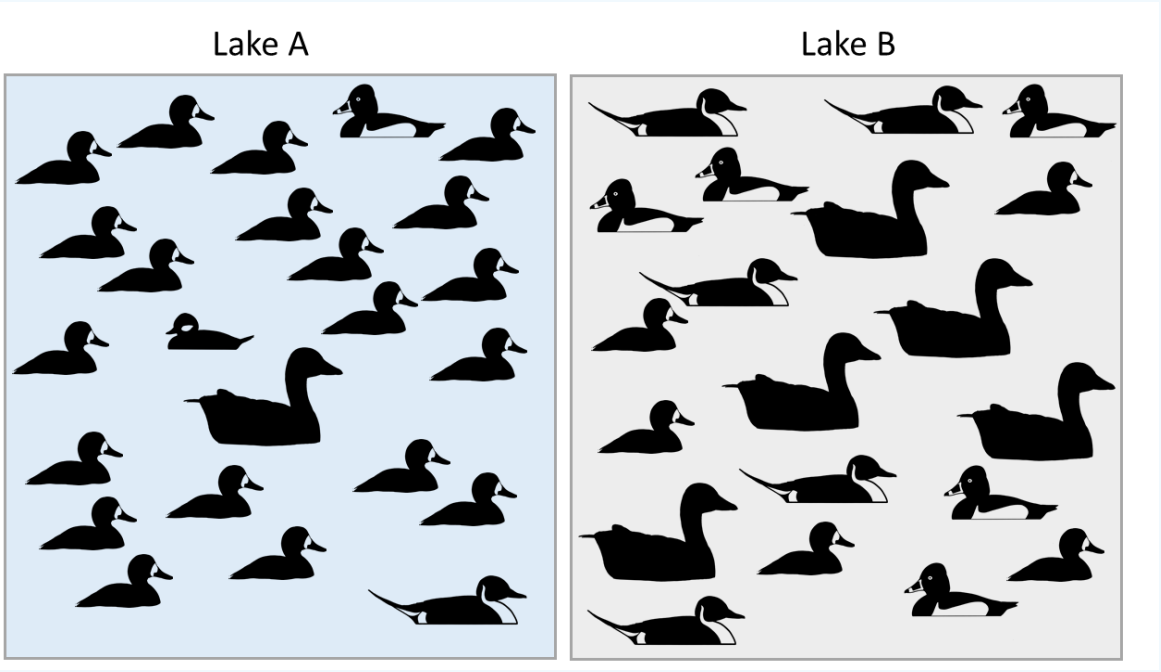
$$J = \frac{H}{H_{\max}} \tag{22.5.3}$$

The value of J ranges from 0 to 1. Higher values indicate higher levels of evenness. At maximum evenness, ***J*** = 1.

J and ***D*** can be used as measures of **species dominance** (the opposite of diversity) in a community. Low J indicates that 1 or few species dominate the community.

Example 22.5.1

Calculate **Simpson's Index**, **Shannon-Weiner Index**, and the **Evenness Index** for waterbirds on two lakes: Lake A, and Lake B. There are 5 species and 25 individuals on both lakes, but are they equally diverse?



Here are the solutions:

Simpson's Index

Species (i)	Lake A			Lake B		
	count (n_i)	n_i/N	(n_i/N)^2	count (n_i)	n_i/N	(n_i/N)^2
 1	1	1/25 = 0.04	0.0016	5	5/25 = 0.2	0.04
 2	1	1/25 = 0.04	0.0016	5	5/25 = 0.2	0.04
 3	1	1/25 = 0.04	0.0016	5	5/25 = 0.2	0.04
 4	1	1/25 = 0.04	0.0016	5	5/25 = 0.2	0.04
 5	21	21/25 = 0.84	0.7056	5	5/25 = 0.2	0.04
S = 5	N = 25	$D = \sum_{i=1}^{S} \left(\frac{n_i}{N}\right)^2$	0.71	N = 25	$D = \sum_{i=1}^{S} \left(\frac{n_i}{N}\right)^2$	0.2

Note that Simpson's Index is often expressed (1-*D*), so the final answers are **0.29** and **0.8**. This makes more intuitive sense: a higher D is more diverse--which is Lake B because it is less dominated by one species.

Shannon-Weiner Index

Species (i)	Lake A				Lake B			
	count (n_i)	p_i	ln(p_i)	$p_i * \ln(p_i)$	count (n_i)	p_i	ln(p_i)	$p_i * \ln(p_i)$
 1	1	0.04	-3.219	-0.129	5	0.2	-1.609	-0.322
 2	1	0.04	-3.219	-0.129	5	0.2	-1.609	-0.322
 3	1	0.04	-3.219	-0.129	5	0.2	-1.609	-0.322
 4	1	0.04	-3.219	-0.129	5	0.2	-1.609	-0.322
 5	21	0.84	-0.174	-0.146	5	0.2	-1.609	-0.322
S = 5	N = 25	$H = -\sum_{i=1}^{S} p_i * \ln p_i$		0.661	N = 25	$H = -\sum_{i=1}^{S} p_i * \ln p_i$		1.61

Again, according to the Shannon-Weiner Index, Lake B is more diverse.

Evenness Index

From above we know that H_{max} is 1.61 (i.e. the highest of the Shannon-Weiner Index values)

The Evenness Index for Lake A is $J = \frac{H}{H_{max}} = \frac{0.661}{1.61} = 0.41$

The Evenness Index for Lake B is $J = \frac{H}{H_{max}} = \frac{1.61}{1.61} = 1$

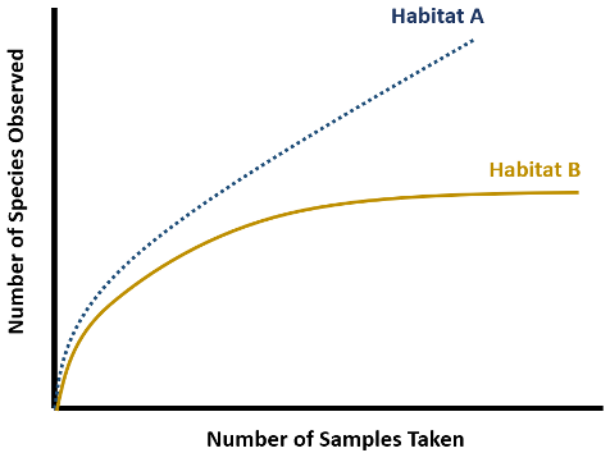
Conclusion

By all three measures, Lake B is more diverse, despite the fact that the two lakes have identical species richness.

Rarefaction Curves

In ecology, rarefaction is a technique to assess species richness from the results of sampling. When sampling various species in a community, the larger the number of individuals sampled, the greater number of species that will be found. Rarefaction allows the calculation of species richness for a given number of individual samples, based on the construction of so-called rarefaction curves. This curve is a plot of the number of species as a function of the number of samples. Rarefaction curves generally grow rapidly at first, as the most common species are found, but the plateau of the curve as only the rarest species remain to be sampled.

Rarefaction curves are necessary for estimating species richness. Raw species richness counts, which are used to create accumulation curves, can only be compared when the species richness has reached a clear asymptote. Rarefaction curves also help to tell us what we *don't know*. If a curve hasn't yet reached its asymptote, there are additional species in that habitat still to discover.



A simplified example of a rarefaction curve. In both habitats, the number of species observed (species richness) increases with the number of samples taken. In Habitat B, the curve eventually saturates (reaches an asymptote), suggesting that the actual species richness of the habitat has been reached. Habitat A, however, has not yet reached its asymptote, so additional sampling would reveal additional new species in this habitat.

Case Study: The Deep Sea of the Mediterranean Basin

From: Danovaro, R., Company, J.B., Corinaldesi, C., D'Onghia, G., Galil, B., Gambi, C., Gooday, A.J., Lampadariou, N., Luna, G.M., Morigi, C. and Olu, K., 2010. Deep-sea biodiversity in the Mediterranean Sea: the known, the unknown, and the unknowable. PloS one, 5(8), p.e11832.

Deep-sea ecosystems represent the largest biome of the global biosphere, but knowledge of their biodiversity is still scant. The Mediterranean basin has been proposed as a hotspot of terrestrial and coastal marine biodiversity, but has been supposed to be impoverished of deep-sea species richness. Danovaro et al. (2010) summarized all available information on benthic biodiversity

(Prokaryotes, Foraminifera, Meiofauna, Macrofauna, and Megafauna) in different deep-sea ecosystems of the Mediterranean Sea (200 to more than 4,000 m depth), including open slopes, deep basins, canyons, cold seeps, seamounts, deep-water corals and deep-hypersaline anoxic basins and analyzed overall longitudinal and bathymetric patterns.

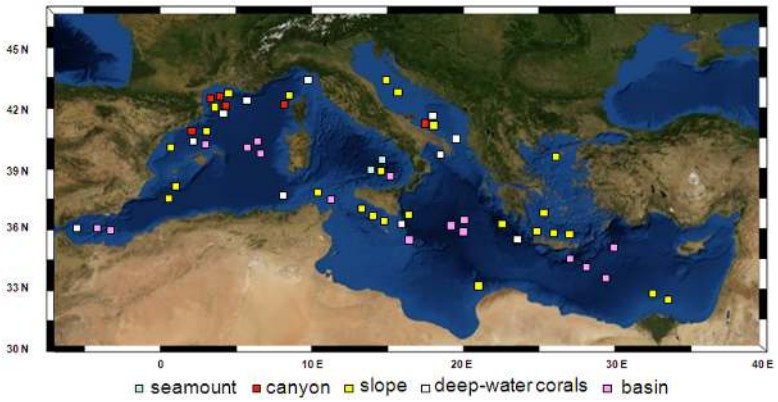


Figure 1. Investigated areas in the Mediterranean basin. Areas include slopes, seamounts, canyons, deep-water corals, and basin.

Danovaro et al. (2010) found that all of the biodiversity components, except Bacteria and Archaea, displayed a decreasing pattern with increasing water depth, but to a different extent for each component. Unlike patterns observed for faunal abundance, highest negative values of the slopes of the biodiversity patterns were observed for Meiofauna, followed by Macrofauna and Megafauna. Comparison of the biodiversity associated with open slopes, deep basins, canyons, and deep-water corals showed that the deep basins were the least diverse. Rarefaction curves allowed for estimation of the expected number of species for each benthic component in different bathymetric ranges. Species were unique across ecosystems, so each ecosystem contributes significantly to overall biodiversity.

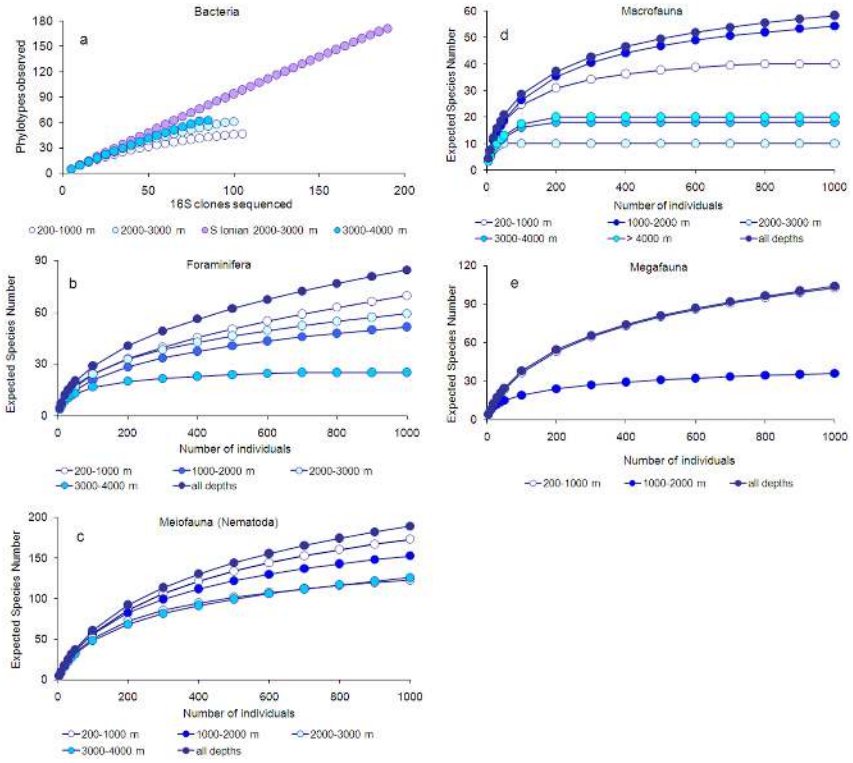


Figure 2. Rarefaction curves for the different components of the deep biota.

Danovaro et al. (2010) estimated that the overall deep-sea Mediterranean biodiversity (excluding prokaryotes) reaches approximately 2,805 species, of which about 66% is still undiscovered. Among the biotic components investigated (Prokaryotes excluded), most of the unknown species are within the phylum Nematoda, followed by Foraminifera, but an important fraction of macrofaunal and megafaunal species also remains unknown. The data in this study provide new insights into the patterns of biodiversity in the deep-sea Mediterranean and new clues for future investigations aimed at identifying the factors controlling and threatening deep-sea biodiversity.

Biodiversity at different scales- Alpha, Beta, and Gamma

Biologists have developed three quantitative measures of species diversity as a means of measuring and comparing species diversity:

- Alpha diversity (or species richness), the most commonly referenced measure of species diversity, refers to the total number of species found in a particular biological community, such as a lake or a forest. Bwindi Forest in Uganda, with an estimated 350 bird species, has one of the highest alpha diversities of all African ecosystems.
- Gamma diversity describes the total number of species that occur across an entire region, such as a mountain range or continent, that includes many ecosystems. The Albertine Rift, which includes Bwindi Forest, has more than 1,074 species of birds, a very high gamma diversity for such a small region.
- Beta diversity connects alpha and gamma diversity. It describes the rate at which species composition changes across a region. For example, if every wetland in a region was inhabited by a similar suite of plant species, then the region would have low beta diversity; in contrast, if several wetlands in a region had plants communities that were distinct and had little overlap with one another, the region would have high beta diversity. Beta diversity is calculated as gamma diversity divided by alpha diversity. The beta diversity for forest birds of the Albertine Rift is about 3.0, if each ecosystem in the area has about the same number of species as Bwindi Forest.

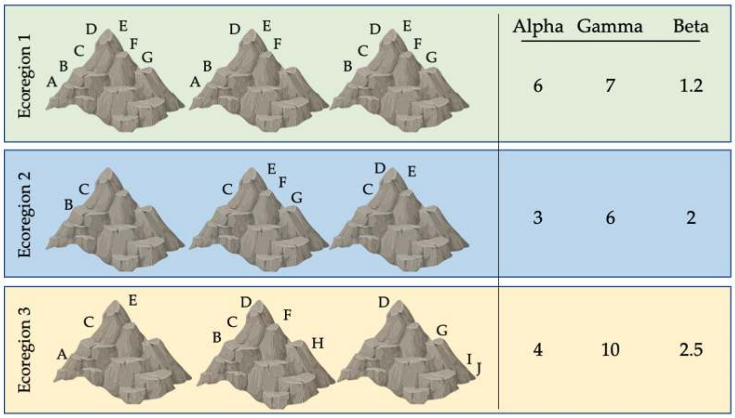


Figure 22.5.1: Biodiversity indices for nine mountain peaks across three ecoregions. Each symbol represents a different species; some species have populations on only one peak, while others are found on two or more peaks. The variation in species richness on each peak results in different alpha, gamma, and beta diversity values for each ecoregion. This variation has implications for how we divide limited resources to maximise protection. If only one ecoregion can be protected, ecoregion 3 may be a good choice because it has high gamma (total) diversity. However, if only one peak can be protected, should a peak in ecoregion 1 (with many widespread species) or ecoregion 3 (with several unique, range-restricted species) be protected? After Primack, 2012, CC BY 4.0.

It is important to note that alpha, beta, and gamma diversity describe only part of what is meant by biodiversity. For example, none of these three terms completely account for genetic diversity, which allows species to adapt as conditions change. It also neglects the importance of ecosystem diversity, which results from the collective response of species to their dynamic environment. However, these diversity measures are useful for comparing different regions, and identifying locations with high concentrations of native species that should be protected.

Functional Diversity and Indigenous Land Use Practices

Case Study Modified from Armstrong, C. G., Miller, J. E., McAlvay, A. C., Ritchie, P. M., & Lepofsky, D. (2021). Historical indigenous land-use explains plant functional trait diversity. Ecology and Society. 26: 6. This article was published under CC BY 4.0.

In addition to species diversity, ecologists are often interested in the trait or functional diversity of a community. A trait is simply any morphological, physiological or phenological feature measurable at the individual level (Reiss et al. 2009). Functional traits are those that define species in terms of their ecological roles - how they interact with the environment and with other species (Diaz and Cabido, 2001).

Functional diversity is a biodiversity measure based on functional traits of the species present in a community. In ocean phytoplankton, for example, these traits usually include body size, tolerance and sensitivity to environmental conditions, motility, shape, and N-fixation ability (Reynolds et al., 2002; Weithoff G. 2003). In terrestrial plant communities, researchers have included more complex traits like rates of growth, nutrient requirements and water uptake (Walker and Langridge, 2002; Barnett et al, 2007). Functional traits are a critical tool for understanding ecological communities because they give insights into community assembly processes as well as potential species interactions and other ecosystem functions. Because there are a greater variety of “roles” being played in a system with higher functional diversity, this measure of diversity has often been linked to higher ecosystem productivity and stability.

Human land-use legacies have long-term effects on plant community composition and ecosystem function and on the diversity of functional traits. Armstrong et al. (2021) studied how plant functional trait distributions and functional diversity are affected by ancient and historical Indigenous forest management in the Pacific Northwest.



Figure 22.5.2: The Village complex of Dałk Gyilakyaw consists of three discrete villages and is the ancestral home of Gitsm’geelm (Ts’msyen) people. Note the dramatic vegetation change between the forest garden and encroaching conifers (“periphery forests”). Photograph: S. Carroll.

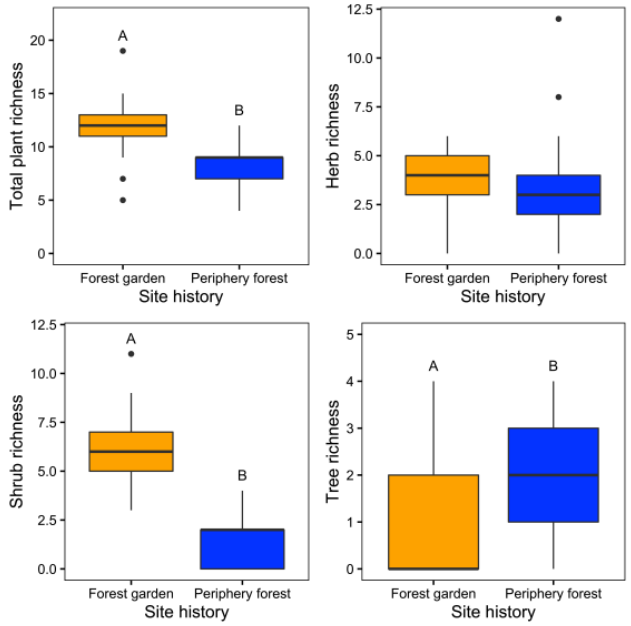


Figure 22.5.3: Total Species Richness and Species Richness by Lifeform. Richness is indicated overall between forest gardens and periphery forests (averaged across the four of the study areas) and among the three growth forms (trees, shrubs and herbs)

For their research into plant functional diversity, Armstrong et al. (2021) compared forest garden ecosystems - managed perennial fruit and nut communities associated exclusively with archaeological village sites - with surrounding periphery conifer forests. To characterize the functional diversity of understory plant communities, they focused on four functional traits: seed mass, shade tolerance, pollination syndrome, and dispersal syndrome. These traits represent important axes of plant life-history variation and can also have important consequences for ecosystem functioning, while also having relevance to ethnobotanical plant uses (Pérez-Harguindeguy et al. 2013). For example, plants with animal-dispersed seeds may be able to disperse long distances and may also contribute to wildlife habitat by providing edible fruits; these plants are also more likely to be eaten by people.

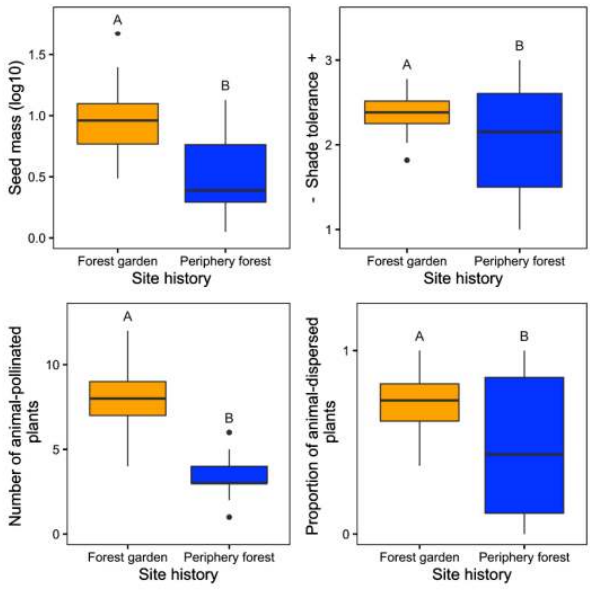


Figure 22.5.4: Functional Trait Measures between Forest Gardens and Periphery Forests. Comparisons of average seed mass, shade tolerance, pollination syndrome, and dispersal syndrome traits for herbs and shrubs across forest gardens and peripheral forests — all are significantly higher in the forest gardens.

Armstrong et al. (2021) found that forest gardens have substantially greater plant and functional trait diversity than periphery forests, even more than 150 years after management ceased. Forests managed by Indigenous peoples in the past now provide diverse resources and habitat for animals and other pollinators and are more rich than naturally forested ecosystems. Although ecological studies rarely incorporate Indigenous land-use legacies, the positive effects of Indigenous land use on contemporary functional and taxonomic diversity found by Armstrong et al. (2021) suggest that Indigenous management practices are tied to ecosystem health and resilience.

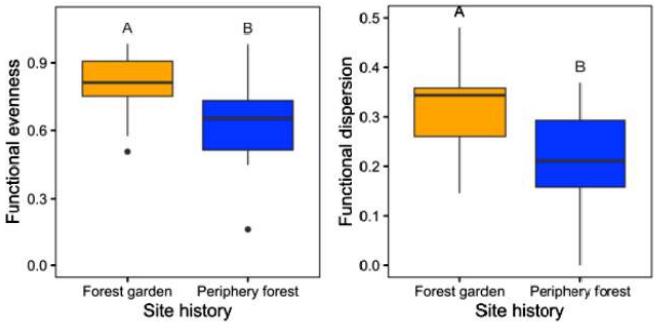


Figure 22.5.5: Functional Diversity Measures between Forest Gardens and Periphery Forests. Functional evenness (the evenness of functional trait distribution in niche space; Villéger et al. 2008) and functional dispersion (the average distance to the abundance-weighted centroid of functional trait values; Laliberté, and Legendre 2010) were significantly greater in forest gardens as compared to periphery forests. Comparisons of functional diversity at forest gardens and peripheral forests.

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22.6: Patterns in Biodiversity

Biodiversity is not evenly distributed on the planet. For example, Lake Victoria in Africa (Figure 22.6.1) contained almost 500 species from a family of fishes called cichlids before the introduction of the **invasive** Nile Perch in the 1980s and 1990s caused a mass extinction. Note that this number does not include species of other fish families. Lake Huron, the second largest of North America's Great Lakes, contains about 79 species of fish, all of which are found in many other lakes in North America.

What accounts for the difference in diversity between Lake Victoria and Lake Huron? Lake Victoria is a tropical lake, while Lake Huron is a temperate lake. Lake Huron in its present form is only about 7,000 years old, while Lake Victoria in its present form is about 15,000 years old. These two factors, latitude and age, are two of several hypotheses that biogeographers have suggested explain biodiversity patterns on Earth.



Figure 22.6.1**:** Lake Victoria in Africa, shown in this satellite image, was the site of one of the most extraordinary evolutionary findings on the planet, as well as a casualty of devastating biodiversity loss. (credit: modification of work by Rishabh Tatiraju, using NASA World Wind software)

Biogeography is the study of the distribution of the world's species both in the past and in the present. The work of biogeographers is critical to understanding our physical environment, how the environment affects species, and how changes in environment impact the distribution of a species. There are three main subfields of biogeography: ecological biogeography, historical biogeography (called paleobiogeography), and conservation biogeography. **Ecological biogeography** studies the current factors affecting the distribution of plants and animals. **Historical biogeography**, as the name implies, studies the past distribution of species. **Conservation biogeography**, on the other hand, is focused on the protection and restoration of species based upon the known historical and current ecological information.

Understanding the global distribution of biodiversity is one of the most significant objectives for ecologists and biogeographers. Beyond purely scientific goals and satisfying curiosity, this understanding is essential for applied issues of major concern to humankind, such as the spread of invasive species, the control of diseases and their vectors, and the likely effects of global climate change on the maintenance of biodiversity (Gaston 2000).

Latitudinal Gradients in Biodiversity

Species richness, or biodiversity, increases from the poles to the tropics for a wide variety of terrestrial and marine organisms Figure 22.6.2. This effect is often referred to as the latitudinal diversity gradient (LDG). The LDG is one of the most widely recognized patterns in ecology. A parallel trend has been found with elevation (elevational diversity gradient), though this is less well-studied. Tropical areas play prominent roles in the understanding of the distribution of biodiversity, as their rates of habitat degradation and biodiversity loss are exceptionally high.

Explaining the latitudinal diversity gradient has been called one of the great contemporary challenges of biogeography and macroecology (e.g. Willig et al. 2003, Pimm and Brown 2004). There is a lack of consensus among ecologists about the mechanisms underlying the pattern, and many hypotheses have been proposed and debated.

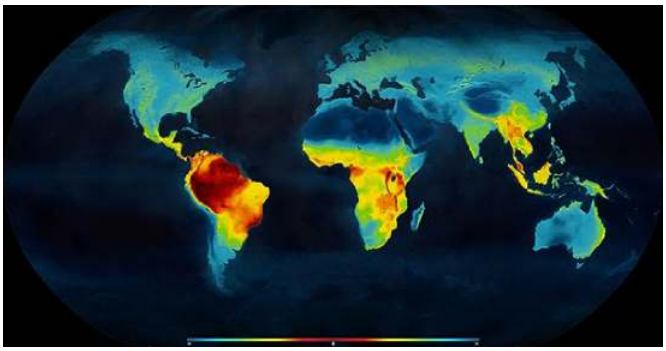


Figure 22.6.2: Map latitudinal gradient of living terrestrial vertebrate species richness (Mannion 2014)

Hypotheses for Latitudinal Gradients

Although many of the hypotheses exploring the latitudinal diversity gradient are closely related and interdependent, the major hypotheses can be split into three general hypotheses. As you will see below, all of these hypotheses have experienced considerable criticisms and debate among members of the scientific community.

Spatial/Area Hypothesis

Mid-domain effect

Using computer simulations, Cowell and Hurt (1994) and Willig and Lyons (1998) first pointed out that if species' latitudinal ranges were randomly shuffled within the geometric constraints of a bounded biogeographical domain (e.g. the continents of the New World, for terrestrial species), species' ranges would tend to overlap more toward the center of the domain than towards its limits, forcing a mid-domain peak in species richness. Colwell and Lees (2000) called this stochastic phenomenon the mid-domain effect (MDE) and suggested the hypothesis that MDE might contribute to the latitudinal gradient in species richness, together with other explanatory factors considered here, including climatic and historical ones. Mid-domain effects have proven controversial. While some studies have found evidence of a potential role for MDE in latitudinal gradients of species richness, particularly for wide-ranging species, others report little correspondence between predicted and observed latitudinal diversity patterns.

Species-energy hypothesis

The species energy hypothesis suggests that the amount of available energy sets limits to the richness of the system. Thus, increased solar energy (with an abundance of water) at low latitudes causes increased net primary productivity (or photosynthesis). This hypothesis proposes the higher the net primary productivity the more individuals can be supported, and the more species there will be in an area. Put another way, this hypothesis suggests that extinction rates are reduced towards the equator as a result of the higher populations sustainable by the greater amount of available energy in the tropics. Lower extinction rates lead to more species in the tropics.

One critique of this hypothesis has been that increased species richness over broad spatial scales is not necessarily linked to an increased number of individuals, which in turn is not necessarily related to increased productivity (Cardillo et al. 2005). The effect of energy has, however, been supported by several studies in terrestrial and marine taxa (Tittensor et al. 2010). The potential mechanisms underlying the species-energy hypothesis, their unique predictions and empirical support have been assessed in a major review by Currie et al. (2004).

Climate-related hypotheses

Another climate-related hypothesis is the climate harshness hypothesis, which states the latitudinal diversity gradient may exist simply because fewer species can physiologically tolerate conditions at higher latitudes than at low latitudes because higher latitudes are often colder and drier than tropical latitudes. Currie et al. (2004) found fault with this hypothesis by stating that, although it is clear that climatic tolerance can limit species distributions, it appears that species are often absent from areas whose climate they can tolerate.

Similarly to the climate harshness hypothesis, climate stability is suggested to be the reason for the latitudinal diversity gradient. The mechanism for this hypothesis is that while a fluctuating environment may increase the extinction rate or preclude

specialization, a constant environment can allow species to specialize on predictable resources, allowing them to have narrower niches and facilitating speciation. The fact that temperate regions are more variable both seasonally and over geological timescales (discussed in more detail below) suggests that temperate regions are thus expected to have less species diversity than the tropics. Critiques for this hypothesis include the fact that there are many exceptions to the assumption that climate stability means higher species diversity. Additionally, many habitats with high species diversity do experience seasonal climates, including many tropical regions that have highly seasonal rainfall (Brown and Lomolino 1998).

Historical/Evolutionary hypotheses

The historical perturbation hypothesis

The historical perturbation hypothesis proposes the low species richness of higher latitudes is a consequence of an insufficient time period available for species to colonize or recolonize areas because of historical perturbations such as glaciation (Brown and Lomolino 1998, Gaston and Blackburn 2000). This hypothesis suggests that diversity in the temperate regions has not yet reached equilibrium and that the number of species in temperate areas will continue to increase until saturated (Clarke and Crame 2003).

The evolutionary rate hypothesis

The evolutionary rate hypothesis argues that higher evolutionary rates in the tropics have caused higher speciation rates and thus increased diversity at low latitudes (Cardillo et al. 2005, Weir & Schluter 2007, Rolland et al. 2014). Higher evolutionary rates in the tropics have been attributed to higher ambient temperatures, higher mutation rates, shorter generation time and/or faster physiological processes (Rohde 1992, Allen et al. 2006), and increased selection pressure from other species that are themselves evolving (Schemske et al. 2009). Faster rates of microevolution in warm climates (i.e. low latitudes and altitudes) have been shown for plants (Wright et al. 2006), mammals (Gillman et al. 2009), and amphibians (Wright et al. 2010). Based on the expectation that faster rates of microevolution result in faster rates of speciation, these results suggest that faster evolutionary rates in warm climates almost certainly have a strong influence on the latitudinal diversity gradient. More research needs to be done to determine whether or not speciation rates actually are higher in the tropics. Understanding whether extinction rate varies with latitude will also be important to whether or not this hypothesis is supported (Rolland et al. 2014).

The hypothesis of effective evolutionary time

The hypothesis of effective evolutionary time assumes that diversity is determined by the evolutionary time under which ecosystems have existed under relatively unchanged conditions, and by evolutionary speed directly determined by effects of environmental energy (temperature) on mutation rates, generation times, and speed of selection (Rohde 1992). It differs from most other hypotheses in not postulating an upper limit to species richness set by various abiotic and biotic factors, i.e., it is a nonequilibrium hypothesis assuming a largely non-saturated niche space. It does accept that many other factors may play a role in causing latitudinal gradients in species richness as well. The hypothesis is supported by much recent evidence, in particular, the studies of Allen et al. (2006) and Wright et al. (2006).

Biotic hypotheses

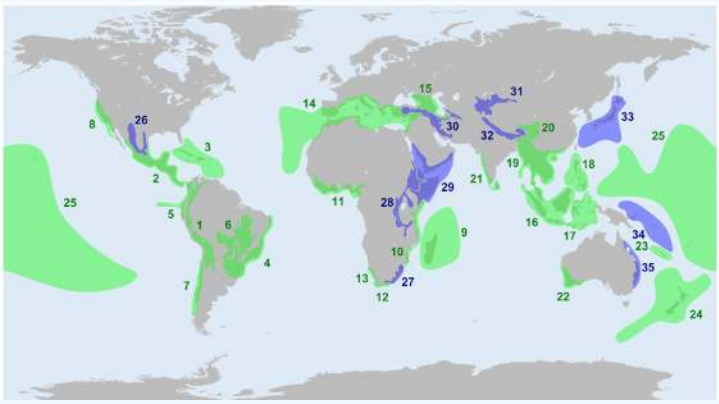
Biotic hypotheses claim ecological species interactions such as competition, predation, mutualism, and parasitism are stronger in the tropics and these interactions promote species coexistence and specialization of species, leading to greater speciation in the tropics. These hypotheses are problematic because they cannot be the ultimate cause of the latitudinal diversity gradient as they fail to explain why species interactions might be stronger in the tropics. An example of one such hypothesis is the greater intensity of predation and more specialized predators in the tropics has contributed to the increase of diversity in the tropics (Pianka 1966). This intense predation could reduce the importance of competition (see competitive exclusion) and permit greater niche overlap and promote higher richness of prey. Some recent large-scale experiments suggest predation may indeed be more intense in the tropics,[12][13] although this cannot be the ultimate cause of high tropical diversity because it fails to explain what gives rise to the richness of the predators in the tropics. Interestingly, the largest test of whether biotic interactions are strongest in the tropics, which focused on predation exerted by large fish predators in the world's open oceans, found predation to peak at mid-latitudes. Moreover, this test further revealed a negative association of predation intensity and species richness, thus contrasting the idea that strong predation near the equator drives or maintains high diversity.[14] Other studies have failed to observe consistent changes in ecological interactions with latitude altogether (Lambers et al. 2002),[1] suggesting that the intensity of species interactions is not

correlated with the change in species richness with latitude. Overall, these results highlight the need for more studies on the importance of species interactions in driving global patterns of diversity.

Biodiversity Hotspots 22.6.1

With the enormous number of species that exist on Earth, it is remarkable that the distribution of these species is so highly concentrated in specific areas. Species richness, the total number of species found in an area, is not evenly distributed around the globe: two-thirds of all known species occur in tropical areas.

In order to prioritize the areas that should be protected, scientists look for areas that are home to a large number of species, especially those species that are under threat of extinction. or that are currently being destroyed at a fast pace. These areas that are particularly important for biodiversity conservation are called biodiversity hotspots. Two things are crucial when determining that a place is a biodiversity hotspot: (i) the number of different species there; and (ii) whether species in that area are endangered or currently being destroyed. Figure 22.6.3 shows the location of 36 biodiversity hotspots, according to the Critical Ecosystem Partnership Fund.



North and Central America	
2	Mesoamerica
8	California Floristic Province
26	Madrean pine–oak woodlands
The Caribbean	
3	Caribbean Islands
South America	
1	Tropical Andes
4	Atlantic Forest
5	Tumbes–Chocó–Magdalena
6	Cerrado
7	Chilean Winter Rainfall-Valdivian Forests
Europe	
14	Mediterranean Basin
Africa	
9	Madagascar and the Indian Ocean Islands
10	Coastal Forests of Eastern Africa
11	Guinean Forests of West Africa
12	Cape Floristic Region
13	Succulent Karoo
27	Maputaland-Pondoland-Albany
28	Eastern Afromontane
29	Horn of Africa

Central Asia	
31	Mountains of Central Asia
South Asia	
19	Indo-Burma, India and Myanmar
21	Western Ghats and Sri Lanka
32	Eastern Himalaya
Southeast Asia and Asia-Pacific	
16	Sundaland and Nicobar Islands of India
17	Wallacea
18	Philippines
22	Southwest Australia
23	New Caledonia
24	New Zealand
25	Polynesia-Micronesia
34	East Melanesian Islands
35	Eastern Australian temperate forests
East Asia	
20	Mountains of Southwest China
33	Japan
West Asia	
15	Caucasus
30	Irano-Anatolian

Figure 22.6.3: The names and locations of current biodiversity hotspots around the globe. The original 25 in green, and added regions in blue (Wikipedia, edited by Andy Wilson).

Scientists have observed that, even though biodiversity hotspots make up only approximately 1.4% of land on our planet, they are home to 60% of Earth's plant, bird, mammal, and reptile species (Possingham and Wilson 2005). Just the endangered species in the tropics accounts for 43% of vertebrates (animals with backbones and their close relatives) and 80% of all amphibians (Marchese 2015). Species found only in a certain geographical area are known as endemic species, and biodiversity hotspots are full of them! For example, the Banana Tree Frog can only be found in Ethiopia, and you will only find lemurs in Madagascar (Herrera 2017). Tropical forests are typically biodiversity hotspots and are usually filled with endemic species. The Upper Amazonia/Guyana Shield, the Congo Basin, and the New Guinea/Melanesian Islands have the highest number of endemic terrestrial (land-living) species on Earth (Cincotta et al. 2000). Figure 22.6.4 shows some examples of biodiversity hotspots and some of their endemic animals and plants.

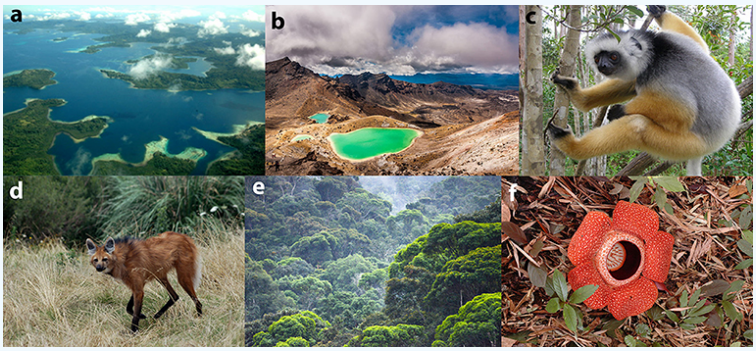


Figure 22.6.4**:** Biodiversity hotspots and some of their endemic species.

(a) Melanesian Islands; (b) Emerald Lakes, New Zealand; (c) Diademed sifaca, one of the endemic lemur species from Madagascar. Mantadia National Park, Madagascar; (d) Maned wolf, the largest canid of South America, a species from the Cerrado hotspot; (e) Atlantic Forest, Caparaó, Brazil; (f) Rafflesia, one of the largest flowers in nature. This particular one, from Borneo, is 80 cm wide [Photo (a): Jim Lounsbury, Wikipedia (https://commons.wikimedia.org/w/inde...?curid=9403460; Photo (b): Marcus Holland-Moritz, Wikipedia (https://commons.wikimedia.org/w/inde...curid=40728121); Photo (c): C. Michael Hogan, Wikipedia (https://commons.wikimedia.org/wiki/F...o_push_off.jpg); Photo (d): Aguara, Wikipedia (https://pt.wikipedia.org/wiki/Lobo-g...le:Aguara1.jpg); Photo (e): Heris Luiz Cordeiro Rocha, Wikipedia (https://commons.wikimedia.org/wiki/F...C3%A2ntica.jpg); Photo (f): Steve Cornish, Wikipedia (https://en.wikipedia.org/wiki/Raffle...esia_80_cm.jpg)].

In addition to land, the waters surrounding these tropical regions are just as important, and equally in danger (Marchese 2015). Tropical coral reefs are currently being threatened by climate change. The change of weather and temperature patterns around the world. and habitat destruction. These areas are some of the most biodiverse ecosystems on our planet! Scientific studies of 3,235 marine species in these areas, including fishes, corals, snails, and lobsters, show that high percentages of these species are at serious risk of becoming extinct (Roberts et al. 2002). Conservation of species living in fresh or seawater is especially difficult, because many bodies of water are interconnected. For example, all the oceans are connected through sea currents that allow the movement of species, minerals, and pollution across the entire globe (Pimm et al. 2014).

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CHAPTER OVERVIEW

Chapter 23: Conservation Biology

Learning Objectives

- Objective 1
- Objective 2
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- Objective 4

23.1: The Science of Conservation Biology

23.2: Policies

23.3: Species-level Conservation

23.4: Protected Areas

23.5: Ecosystem Restoration

23.6: Economic Influences on Conservation

23.7: Individual Choices

Summary

Summary to be added

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23.1: The Science of Conservation Biology



Figure 23.1.1: East Africa's great migration is one of the most famous wildlife spectacles on Earth. Each year, tens of thousands of tourists from around the world flock to the region to see the 1.7 million common wildebeest (*Connochaetes taurinus*, LC) and hundreds of thousands of other plains mammals make their way from Tanzania's Ngorongoro Conservation Area, through the Serengeti Plains, to Kenya's Maasai Mara National Reserve. "Wildebeest Migration in Serengeti National Park, Tanzania" by Daniel Rosengren is licensed under CC BY 4.0.

Popular interest in protecting biological diversity—which describes the amazing range of species, genetic diversity within each species, and the multitude of Earth's complex biological communities with their associated ecosystem processes—has intensified during the past few decades. During this time, scientists and the public have recognized that biological diversity (often shortened to biodiversity) is being lost at increasing rates. Across the world, human activities are destroying ecological communities that have developed over millions of years. Over the next several decades, thousands of species and millions of populations will likely go extinct.

The fundamental driver of all the biodiversity losses we are currently witnessing is a rapidly expanding human population coupled with increased consumptive needs. In 1850, after roughly 300,000 years of *Homo sapiens* on the planet, there were around 1 billion people on Earth. By 1987, not even 140 years later, the world's human population had surpassed 5 billion. By 2017, there were 7.5 billion humans globally, of which over 1 billion lived in Sub-Saharan Africa (World Bank, 2019). With this many people, the human population grows by tens of millions of people each year, even with modest population growth Figure 23.1.2 . To make matters worse, Sub-Saharan Africa has the fastest population growth rate in the world, with a projected human population estimate of over 4 billion people by the year 2100—a number that is well beyond the ecological capacity of the region to support.

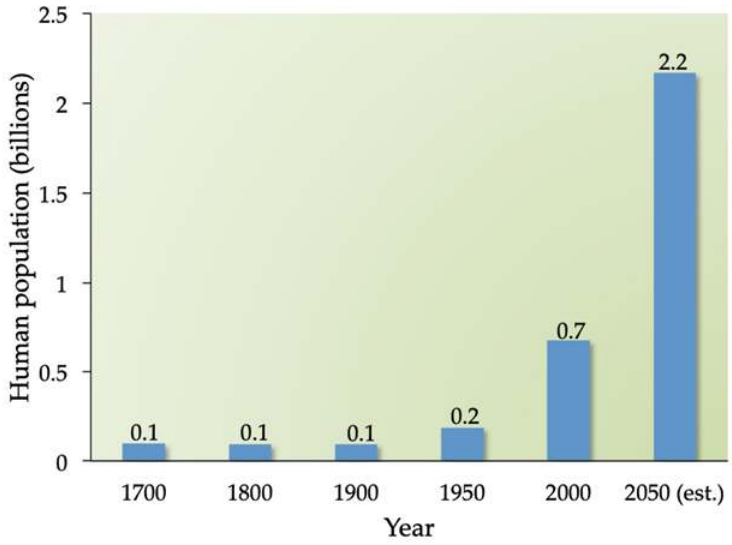


Figure 23.1.2: Sub-Saharan Africa's human population crossed the 1 billion mark in 2015. At the current annual population growth rate of 2.7%, more than 28 million people will be added to the region in 2019. This number will escalate each subsequent year as increases are compounded. *Sources: Biraben, 2003; World Bank, 2019, CC BY 4.0.*

To survive and prosper, people use natural resources. They harvest and use oil, water, and wildlife products, and convert natural ecosystems for agriculture, cities, roads, and industrial activities. This consumption, which reduces natural habitat and the associated wildlife populations, is intensifying because of the demands of a rapidly increasing human population. Consumption of resources also increases as countries develop and industrialize: the average citizen of the USA uses five times more resources than the average global citizen, 11 times more than the average Chinese citizen, and 32 times more than the average Kenyan citizen (Worldwatch Institute, 2015). This growth in the number of humans, together with their ever-more-intensive use of natural resources, is the fundamental driver behind most current species extinctions.

For conservation biologists and other nature lovers, the widespread extinction of species and destruction of natural ecosystems are incredibly discouraging.

Conservation Biology as a Discipline

As a distinct scientific field, conservation biology is an integrated, multidisciplinary subject that developed in response to the challenge of preserving populations, species, ecosystems, and biological interactions. The main aim of conservation biology is to ensure the long-term preservation of biodiversity. To achieve its aim, conservation biology has set three goals:

- To document Earth's biological diversity.
- To investigate how humans influence species, evolution, and ecosystem processes.
- To investigate practical approaches to protect and restore biological communities, maintain genetic diversity, and prevent the extinction of species.

The first two goals describe typical scientific research investigating objective facts. The third goal, however, is a part of what makes conservation biology a normative discipline; that is, conservation biology incorporates human values, not just facts, to understand and achieve its value-laden goals (Lindenmayer & Hunter, 2010). In this sense, conservation biology is related to environmentalism, in which people aim to protect the natural environment for its own sake. However, conservation biology is at its core a scientific discipline; it is founded on scientific principles. This is not to say you must be a scientist to practice conservation biology; there are many people who are not scientists who apply the principles of conservation biology in their professional and personal lives.

The emergence of conservation biology as a distinct scientific field in the 1970s has given rise to the formation of various formal societies representing the field in a united voice. Most notable among these is the Society for Conservation Biology (SCB, Figure 23.1.3), which is a non-profit international professional organization with a mission to advance "the science and practice of

conserving the Earth's biological diversity". To facilitate opportunities where like-minded people can share ideas locally, the SCB has regional branches, including an active Africa Section (http://conbio.org/groups/sections/africa) which hosts regular conferences. In addition to the SCB, a great number of other local, national, and regional conservation organizations also exist and act as mouthpieces for grassroots movements and as custodians of nature. Many of these groups focus on specific animals or local protected areas. Others organically adapt their missions and visions in response to a specific need or threat. For example, established in 1913 as an exchange forum between collectors of rare plants, the Botanical Society of South Africa now actively works toward protecting those rare plants in their natural habitats.



Figure 23.1.3**:** The logo of the Society for Conservation Biology (SCB) has several layers of symbolism. Enclosed in the circle of life are ocean waves, representing change. The bird symbolises beauty, and the leaves (the bird's wings) remind us of nature's productivity. Image courtesy of SCB, all rights reserved.

In recent years, conservation practice has evolved from just a plan to save the environment to a vision that includes sustainable development and social justice.

Conservation biology also has a history of adapting to new challenges. The very first conservation activities, in Africa and beyond, were geared towards securing the rights to valuable natural resources for people in powerful positions, such as kings and tribal chiefs, enforced through a strictly adherence to cultural norms and customary laws. But as a growing human population expanded its influence on the environment, and wildlife started to decline, earliest conservation models gradually shifted towards fortress conservation approaches (Wilshusen et al., 2002) which aimed to shield wildlife from people by setting aside protected areas where human activities were strictly controlled.

Today, however, as human populations are exploding, and consumption is increasing, even protected areas are increasingly unable to withstand the multitude of threats to biodiversity that ignore property boundaries and political borders. In response, fortress conservation approaches are beginning to make way for large-scale integrated activities that highlight the social and economic benefits of biodiversity conservation. To do this, new alliances are being formed and new agendas are being established, such as those that directly link human health with environmental health (Box 23.1.1). These integrated conservation philosophies that pursue strategies that benefit both humans and biodiversity show much promise because they focus on fundamental extinction drivers, and advocate for more inclusive sustainable development. In this way, the practice of conservation has evolved from just a plan to save the environment to a vision that accomplishes its goals through sustainable development and social justice.

Yet, as we consider how to best invest limited conservation resources, some difficult questions arise. With seemingly more work to be done than can be accomplished, should we let some species go extinct (Bottrill et al., 2008)? Which species? Who decides? How can we even dare to think that we can play god? Such questions predictably bring about strongly opinionated and emotional debate (Soulé, 2013 vs. Marvier, 2014; Tallis & Lubchenco, 2014). Given the successful track record of fortress conservation initiatives in preventing extinctions despite limited budgets (Young et al., 2014), as well as the promising progress of more complex people-centred initiatives (Pooley et al., 2014), it seems clear that conservation relies on some balance between these two conservation philosophies (Sodhi et al., 2011). Conservation biologists of tomorrow will be able to fine-tune the balance between these strategies by closely inspecting the successes and failures of our actions today.

Box 23.1.1 Conservation Through Public Health: A Case Study

Gladys Kalema-Zikusoka

Conservation Through Public Health,

Kampala, Uganda.

http://www.ctph.org

Conservation Through Public Health (CTPH) is a grassroots non-governmental organization (NGO) and non-profit that promotes biodiversity conservation by enabling people, wildlife, and livestock to coexist. The organization was founded in 2003 after fatal scabies skin disease outbreaks in mountain gorillas (*Gorilla beringei beringei*, EN) were traced to people living around Bwindi Impenetrable National Park, Uganda, who had limited access to basic health services (Kalema-Zikusoka et al., 2002). Since then, CTPH has contributed to conservation and sustainable development in Africa by improving human and animal health and welfare in and around protected areas.

One of the main goals of CTPH is to reduce disease transfer between humans and gorillas. We accomplish this through an integrated population, health, and environment (PHE) program that was established in 2007 with funding from the US Agency for International Development (USAID). As a first step, piloted around Bwindi, CTPH held consultative meetings with local leaders, during which at least one Village Health and Conservation Team (VHCT) volunteer was selected from each village and two from each parish (consisting of 11 villages) to oversee distribution of family planning supplies. This initiative rapidly expanded into a sustainable social service delivery network that promotes family planning, hygiene, and sanitation. The network resulted in a 20% to 60% (national average is 30%) increase in new users to modern family planning, and a 10% to 60% increase in adoption of hand washing facilities at homes visited by VHCTs. VHCT volunteers also refer people suffering from infectious diseases and malnutrition to local health centres and promote more sustainable alternative livelihoods. Another group of community volunteers, the “Human and Gorilla Conflict Resolution” (HUGO) team, in turn collect gorilla faecal samples left on communal land to monitor their health Figure 23.1.4, and visually monitor gorillas for clinical signs of disease inside and outside protected areas (Gaffikin & Kalema-Zikusoka, 2010). In the process, we have seen reduced disease incidences in the gorillas, reduced conflict between people and gorillas, and improved attitudes toward conservation. One unintended outcome has been increased gender equality: men are now more involved in family planning, and women are more involved in natural resource management.



Figure 23.1.4**:** A park ranger from the Uganda Wildlife Authority teaching HUGO community volunteers how to collect faecal samples from gorilla night nests during a CTPH training workshop. Photograph by CTPH, CC BY 4.0.

Our experience in initiating and managing PHE programs for the past 10 years has taught us several lessons. One of the most important lessons to ensure project sustainability is to regularly engage with local leaders and the government. The Uganda Wildlife Authority, Uganda’s Ministry of Health, and local health centres all attend CTPH meetings with VHCTs. Attendance

by and representation of these groups not only informs them of our activities, but also provides a platform to inform or train the VHCTs in what they would like them to disseminate to the local communities.

We have also learnt that PHE-implementing partners and projects need to be well-suited to each other and each site; this remains true even though health needs are often the same, regardless of the location. For example, at Mount Elgon National Park in Uganda, we found that training VHCTs in reducing conflict with park management played a key role in changing community attitudes toward conservation. In contrast, at Virunga National Park, Democratic Republic of the Congo (DRC), we found that VHCTs needed to work more closely with local health centres to prevent disease transmission between people and gorillas, and to promote family planning in a largely Catholic country.

Lastly, we found that establishing income-generating projects for groups rather than individuals was key to sustaining VHCT networks and program goals beyond donor funding cycles where we have had no volunteer dropouts in the first 10 years of initiating the PHE program. These key components were accomplished by initiating livestock group enterprises and by encouraging VHCT volunteers to invest generated income into Village Saving and Loan Associations (see http://www.care.org/vsla).

The Role of Conservation Biologists

While there are a few extinctions that have only one cause, more generally, extinctions occur because several factors acted simultaneously and/or sequentially. Blaming a certain industry or specific group of people for an extinction (or other biodiversity loss) is thus simplistic, ineffective, and often counter-productive. Though challenging, a better approach would be to better understand how local, national, and international links led to those losses, and to find viable alternatives to prevent it from happening again. To succeed in this challenge, conservation biologists should strongly consider taking on one or more of several roles:

- Conservation biologists should be curious. The world around us is full of natural wonders waiting to be discovered. These discoveries underpin conservation action, by allowing us to define all the different components of biodiversity, enabling us to better understand the needs of different species, and providing us with opportunities to celebrate our conservation successes.
- Conservation biologists must be good listeners. Sometimes, the only difference between attracting a new ally and making an enemy, or between developing a landscape and saving a species from extinction, is the way we communicate. Conservationists must be careful and respectful listeners, especially to opposing perspectives. Careful listening is particularly important in rural areas, where villagers often have practical concerns related to their daily contact with wildlife, such as staying safe and preventing crop damage and livestock loss. Quite often, those villagers may also have unique insights into wildlife ecology that could prove valuable in local conservation measures.
- Conservation biologists must be law-abiding citizens. Activities that involve wildlife and ecosystems are regulated by laws and regulations. These laws are important because ethical boundaries differ from person to person—activities acceptable to one group of people may be considered harmful by another. As conservation biologists, abiding by environmental laws is especially important if we want others to take those laws seriously.

  Laws are important because ethical boundaries differ from person to person—activities acceptable to one person may be immensely harmful to another.

- Conservation biologists should become effective communicators. They should be able to discuss the problems facing biodiversity in depth, as well as the consequences of losing biodiversity, to as broad a range of people as possible. Groups like hunters, community leaders and organizers, and church leaders may be interested in participating in conservation efforts once they recognize that their activities, health, and emotional well-being depend on conservation action.
- Conservation biologists could become politically active leaders, so that they can influence public opinion and policy. As a starting point, those interested in this role can join a conservation organization to learn more about broader issues. They could also use their personal networks to form alliances with lawyers, citizen groups, and politicians.
- Conservation biologists could become pro-active land managers. Those taking on this task must be willing to walk on the land and go out on the water to find out what is really happening. They should also talk with local people to communicate their knowledge to others in ways that are clear and easily understood.
- Above all, a conservation biologist must be honest. To encourage effective action, both from the public and through policy, conservationists must present arguments backed by reliable evidence. To do otherwise, conservation biologists could lose

credibility, which would very likely delay or even compromise conservation efforts.

It is worth taking a moment to distinguish between two important pillars of conservation action, namely conservation advocacy and conservation science. Conservation advocacy describes the roles that conservation biologists adopt to guide social, political, and economical systems towards a personally-preferred outcome—adopting environmentally-friendly practices; incorporating these activities makes conservation biology a normative discipline. Conservation science, in contrast, describes activities that conservation biologists undertake to generate knowledge, like objectively describing biodiversity and measuring biodiversity's response to stressors and safeguards. While conservation advocacy and conservation science often support and inform each other as to the next steps required for "doing conservation", it is important to distinguish between these two pillars to ensure that policymakers and other stakeholders in the environment understand when we advocate for personal preferences and when we offer objective findings (Rykiel, 2001; Lackey, 2007; Nelson & Vucetich, 2009). The next section will further expand on the importance of science in conservation biology.

The Importance of Scientific Methods

The field of conservation biology applies scientific methods to achieve its goals. Like the medical sciences, which apply principles from physiology, anatomy, and genetics to problems of human health, conservation biologists solve biodiversity problems using principles from fields, such as mathematics, veterinary medicine, social sciences, and several natural sciences (Figure 23.1.5). Conservation biology differs from these and other component disciplines in that its primary goal is the long-term preservation of biodiversity. Unlike many other scientific fields, conservation biology can also be described as a crisis discipline (Soulé, 1985; Kareiva & Marvier, 2012). That is, conservation biologists are often required to take creative steps to respond to imminent threats, typically without complete knowledge of the systems requiring attention. Conservation scientists must also articulate long-term visions for conservation beyond solving immediate problems.

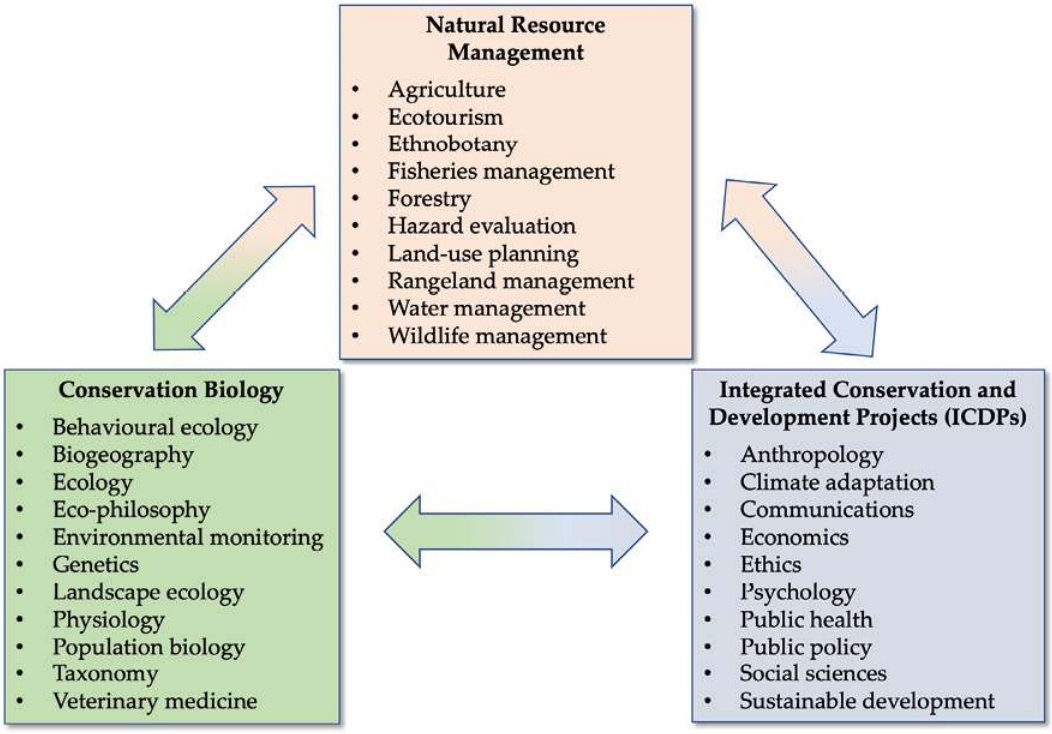


Figure 23.1.5**:** Conservation biology draws from many other sciences to protect biodiversity. It is closely related to natural resource management, which aims to manage biodiversity primarily for the benefit of humans. Integrated conservation and development projects (ICDP) are projects that manage nature for the benefit of both humans and biodiversity. After Kareiva and Marvier, 2012; Temple, 1991, CC BY 4.0.

To be effective, conservation biologists must demonstrate the relevance of their findings to a range of stakeholders. To be successful in this task, the importance of sound scientific principles cannot be over-emphasized. Nature is a complex network of many interdependent connections and feedback loops. Science is underpinned by principles that provide conservationists the

necessary quantitative and qualitative tools to better measure and control for all these different aspects of biodiversity. Such measurements allow us to gain a better understanding of complex natural systems, and the consequences of human activities. Reliable, unbiased data obtained from sound and transparent scientific methods also facilitate policymaking that is too often based on value judgments by non-experts who must balance many needs and different sources of information (Ntshotsho et al., 2015).

One of the cornerstones of modern science is to identify a hypothesis (a proposed explanation for a specific observation) to evaluate. The best hypotheses, often expressed as goals or objectives, are usually those that are SMART:

Specific: not overly general

Measurable: has both units and a method of measurement

Attainable: realistic to achieve

Relevant: related to what needs to be accomplished

Time-bound: achievable within a specific timeframe

Identifying SMART goals and objectives is an essential aspect of conservation biology. Without such benchmarks, practitioners cannot know whether their tasks were successful, or when management actions should be adjusted to achieve success. While this may seem obvious, many previous conservation projects have failed because biologists neglected to set SMART goals and objectives (Tear et al., 2005). While lofty, “We’re going to save all species” is not a SMART conservation goal because it is overly general, hard to measure, unrealistic, and not time-bound. In contrast, “We want to protect 25% of our country’s wetlands within the next 10 years” is a SMART goal because it sets a very clear and measurable objective. In general, it is wise to set smaller short-term (e.g. quarterly), and medium-term (e.g. annual) goals as one works towards long-term (e.g. 5–10 years) objectives; this allows one to constantly assess progress, which in turn provides opportunities for celebrations and strategic adjustments as and when needed.

Conservation biology’s ethical principles

Conservation biology rests on a set of underlying ethical principles that is generally agreed upon (Soulé, 1985) and can be summarized as follows:

- The diversity of species and biological communities should be preserved: Most people appreciate biodiversity. Hundreds of millions of people visit national parks, game reserves, zoos, botanical gardens, and aquaria each year. They spend money and take actions to protect these places and species. People also recognize that biodiversity has economic value, whether through tourism, consumption, or other services.
- The untimely extinction of populations and species should be prevented: Throughout history, species have occasionally died off as a result of natural, non-human causes. The loss of a local population was generally temporary until a new population established itself through dispersal. However, human activities have increased the rate at which species are going extinct by more than a hundredfold. Meanwhile, there is no similar increase in the rate at which new populations and species are being created.
- Ecological complexity should be maintained: In complex natural environments, biodiversity expresses many of its most valuable features and interactions. Although the biodiversity of species may be partially preserved in captivity, maintaining ecological complexity requires that natural areas be preserved.
- Evolution should continue: Evolution creates new species, increases biodiversity over time, and facilitates adaptation to changing environmental conditions. People can help preserve these evolutionary processes by maintaining genetic diversity in wild populations and allowing populations to exchange genetic material. In captivity, many natural evolutionary processes do not occur, which can hamper survival when species are reintroduced in the wild.
- Biodiversity has intrinsic value: The value of species, communities, and ecosystems does not depend on their utility to people. They are intrinsically valuable on their own, with unique evolutionary histories and ecological roles. There are certain iconic

species that people simply want to have around, but other, lesser-known species or species seen as problematic to people are not less valuable.

These principles are not absolute, nor are conservation biologists required to agree with them—they are actively discussed and debated. But many individuals and organizations agree with two, three, or all the principles, and support conservation efforts.

Box 23.1.2 Biodiversity: Can Humanity be Saved?

Nkengifor Nkeshia Valery, Regina International Cameroon, Member of Union Farms of Africa, Yaoundé, Cameroon.

What happened over the past 200 years that we have arrived where we are? How did we get to this modern paradox? A society where we cherish comfort at the cost of the ever-increasing destruction of our planet. Never in the history of humanity has the environment been degraded to the point that even the air we breathe has become cancerous. Animals are exploited by industries at an alarming rate and those remaining are killed to enrich a privileged few. And all this evil happens with our complicity as indirect consumers. Our inheritance from God, the source of all our nourishment, does not belong to us. Yet it has been bought and exploited by multinational corporations and financial markets that hinder us from cultivating sustainably. We are pushed to feed ourselves and our crops with chemical products that are dangerous to our long-term health. We are also experiencing the start of the sixth mass extinction episode of biodiversity (Ceballos et al., 2017). As a result, the natural world has declared World War III against humanity. This is a war fought not by nation against nation, but that the environment has declared against the whole human race.

This war condemns us to live in an illusion of freedom; we are, in fact, destroyed at an increasing rate by different dangerous diseases and rendered slaves of the polluted environments that we blindly accept. The question we need to ask is not whether we should act to save our planet, but what future and meaning we are going to give the word “HUMANITY”. We are all actors in a civilization that we are constructing; to quote the Indian leader Mahatma Gandhi: “If we could change ourselves, the tendencies in the world would also change. As a man changes his own nature, so does the attitude of the world change towards him. […] We need not wait to see what others do”. Let us pause and ask ourselves what we want the future to say of us. Are we a destructive generation, or a generation that is ready to sustainably preserve its biodiversity? It is a question every reader needs to ponder. The future is judging no one and blaming no one, but it needs us to change our habits towards protecting the world’s biodiversity.

To change our attitude and make the world a better place, I drafted the following poem with passion to see my words become action for every lover of biodiversity

WORLD CHANGERS

We are a people of peace called forth out of humanity into restoring life to our natural habitat. We are governed and guided by a sense of sustainability. Conservation and protection is our priority in all things at all times we are led and driven by the spirit of an environment free of pollution we are called to effect and affect every life that we come in contact with towards the sustainable development of the environment.

We are called by humanity to be world changers we refuse to conform with the thinking pattern of the world system because we are world changers.

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23.2: Policies

National and State Laws

Within many countries there are laws that protect endangered species and regulate hunting and fishing. For example, the **Endangered Species Act** (ESA) was enacted in 1973 in the United States. The ESA does not automatically protect species categorized as threatened on the Red List. Instead, the U.S. Fish and Wildlife Service (FWS), which enforces the ESA, assesses candidates for protected status as threatened or endangered (figure 23.2.a). Consideration of candidate species can be initiated by the FWS itself or at the request of the public. Through the Species Status Assessment Framework, the FWS compiles biological data, such as habitat and population information and current threats to the species. This biological data is used to inform decisions.



Figure 23.2.a: Public Affairs Specialist for the U.S. Fish and Wildlife Service, Joanna Gilkeson, takes photos of federally endangered San Diego fairy shrimp in a vernal pool in Otay Mesa, California. Vernal pools are shallow seasonal ponds, and vernal pool species are uniquely adapted to changes in water availability. Image by Maideline Sanchez/USFWS (public domain).

Once a species is listed, the FWS is required by law to develop a management plan to protect the species and bring it back to sustainable numbers. The ESA, and others like it in other countries, is a useful tool, but it suffers because it is often difficult to get a species listed or to get an effective management plan in place once a species is listed.

The 1972 **Marine Mammals Protection Act** prohibits the "take" of marine mammals—including harassment, hunting, capturing, collecting, or killing—in U.S. waters and by U.S. citizens on the high seas. The act also makes it illegal to import marine mammals and marine mammal products into the United States without a permit.

State laws can also aid in conservation. Through **California Endangered Species Act** (CESA), originally passed in 1970 and subsequently amended, the California Fish and Game Commission assesses species to be listed as threatened or endangered by the state. A listed species, or any part or product of the plant or animal, may not be imported into the state, exported out of the state, "taken" (killed), possessed, purchased, or sold without proper authorization.

Note that endangered is a subcategory of threatened on the Red List, but for ESA and CESA, threatened and endangered are separate categories, with the latter representing at the greater risk of extinction.

International Agreements

The **Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES)** treaty came into force in 1975. The treaty, and the national legislation that supports it, provides a legal framework for preventing listed species from being transported across nations' borders, thus protecting them from being caught or killed when the purpose involves international trade.

Species can be listed in one of three CITES appendices. Trade is banned for Appendix I species, which are threatened with extinction. For example the trade of ivory is banned by CITES. Trade is regulated for Appendix II species, such as the meat and shells of the queen conch or big-leaf mahogany (figure 23.2.*b*). Appendix III species are protected in at least one country, and the local government needs a coordinated response through CITES. For example, several species of red and pink corals have been added to Appendix III at the request of China.



Figure 23.2.*b*: Big-leaf mahogany (*Swietenia macrophylla*) timber is used to make furniture, musical instruments, boats, and other products. It listed in CITES Appendix II, meaning that it is regulated. Specifically, a permit is required to ship big-leaf mahogany timber. Image by Forest and Kim Starr (CC-BY).

Approximately 35,800 species are protected by the CITES. The treaty is limited in its reach because it only deals with international movement of organisms or their parts. It is also limited by various countries' ability or willingness to enforce the treaty and supporting legislation.

The **Migratory Bird Treaty Act** (MBTA) is an agreement between the United States and Canada that was signed into law in 1918 in response to declines in North American bird species caused by hunting. The Act now lists over 800 protected species. It makes it illegal to disturb or kill the protected species or distribute their parts (much of the hunting of birds in the past was for their feathers). Examples of protected species include northern cardinals, the Red-tailed Hawk, and the American Black Vulture.

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23.3: Species-level Conservation

Some conservation efforts center around a single species. Often this is a charismatic species that elicits public interest, such as tigers, sea otters, or the California Condor. The specific approach depends on the specific threats to the focus species. When California Condor population size plummeted, leaving only 23 individuals, they were relocated into a controlled environment and provided with optimal conditions for reproduction. This is called **captive breeding**. Individuals have since been **reintroduced** into the environment. One threat to the species was lead from bullets that were entering the food chain and ultimately poisoning the California Condor. Public education and providing lead-free bullets was thus another component of their conservation plan. By 2016, the population size increased to 446 individuals, with 276 of those living in the wild.

When disease puts species at risk, vaccination may be part of the conservation plan. For example, the black-footed ferret of the Great Plains is threatened by sylvatic plague as well as habitat loss. In response, peanut buttered-flavored oral vaccines were distributed over their habitats. Conservation efforts also focused on captive breeding and reintroduction. Once thought to be extinct, there are now several hundred black-footed ferrets in captivity and similar numbers in the wild (figure 23.3.*a*).

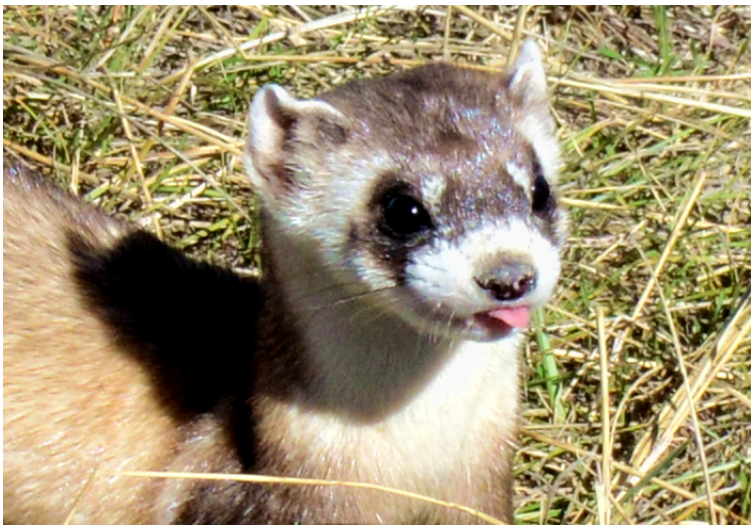


Figure 23.3.*a*: A black-footed ferret kit at the National Black-footed Ferret Conservation Center in Colorado. Image by Ryan Moehring/USFWS (CC-BY)

Protecting or restoring habitat is another component of species-level conservation. For example, the Northern Spotted Owl lives in old-growth forests. Protecting intact old-growth forests and restoring forest habitat is thus critical to their success. This is accompanied by removal of the Barred Owl, an invasive that competes with the Northern Spotted Owl. Similarly, removal of the invasive iceplant *Carpobrotus edulis* from California coasts, restores conditions for endangered dune vegetation (figure 23.3.*b*-d). In other cases, habitat restoration involves promoting populations of native species that support those at risk, such as promoting vegetation that provides food and shelter for waterfowl.



Figure 23.3.*b*: Vegetation at Martin Dunes in California. Iceplant is visible in the forefront. Photo by USFWS (public domain).



Figure 23.3.*c*: *Carpobrotus edulis* is an invasive iceplant that forms thick mats and outcompetes coastal vegetation. Image by Dr. Dwayne Meadows, NOAA/NMFS/OPR (public domain).



Figure 23.3.*d*: Removal of the iceplant restores habitat for endangered species, such as Menzies' wallflower. Image by Gordon Leppig & Andrea J. Pickart, FWS (public domain).

Seemingly unimpressive species can still serve vital ecological roles. For example, the delta smelt is an important food source for larger fish species. Additionally, it serves as an **indicator species** because the health of its populations reflect overall ecosystem health. While the delta smelt has been a focus of species-level conservation, non-charismatic species are often overlooked. In fact, a 2007 study by Colléony and colleagues found that people more often donated to conservation efforts for species that were more similar to humans rather than choosing those that were at greatest risk of extinction. Broad approaches such as establishing protected areas and ecosystem restoration benefit charismatic and non-charismatic species alike. Additionally, broad approaches protect unidentified and species that have not been assessed.

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23.4: Protected Areas

It is important to protect natural areas for several reasons. Some people feel a cultural or spiritual connection to the wilderness. Every year, millions of people visit recreational lands such as parks and wilderness areas to experience attractions of the great outdoors: hiking among the giant sequoias in California, traveling on a photo safari in Kenya or just picnicking at a local county park. Besides providing people with obvious health benefits and aesthetic pleasures, recreational lands also generate considerable tourist money for government and local economies. Outdoor recreation activities such as hiking and camping benefit tourist industries and manufacturers of outdoor clothes and equipment.

Establishment of preserves is one of the key tools in conservation efforts. A **preserve** is an area of land set aside with varying degrees of protection for the organisms that exist within the boundaries of the preserve (figure 23.4.a). Governments or private organizations establish nature preserves. In 2016, the IUCN estimated that 14.7 percent of Earth's land surface was covered by preserves of various kinds. This area is large, but only 20% of the key biodiversity areas identified by the IUCN were sufficiently protected.



Figure 23.4.a: Mequon Nature Preserve in Wisconsin. Image by Jennifer Tomaloff (CC-BY-NC-SA).

There has been extensive research into optimal preserve designs for maintaining biodiversity. Preserves can be seen as "islands" of habitat within "an ocean" of non-habitat. In general, large preserves are better because they support more species, including species with large home ranges; they have more core area of optimal habitat for individual species; they have more niches to support more species; and they attract more species because they can be found and reached more easily. One large preserve is better than the same area of several smaller preserves because there is more core habitat unaffected by less hospitable ecosystems outside the preserve boundary. For this same reason, preserves in the shape of a square or circle will be better than a preserve with many thin "arms." If preserves must be smaller, then providing wildlife corridors between two preserves is important so that species and their genes can move between them. All of these factors are taken into consideration when planning the nature of a preserve before the land is set aside. In addition to the physical specifications of a preserve, there are a variety of regulations related to the use of a preserve. These can include anything from timber extraction, mineral extraction, regulated hunting, human habitation, and nondestructive human recreation.

The public lands described below differ in their level of protection. For example, national parks and forests allow camping whereas wildlife refuges place more limitations on human activities.

Wilderness Areas

Wilderness areas, comprise ecosystems in which human activity has not significantly affected the plant and animal populations or their environment. Natural processes predominate. According to the "Wilderness Act of 1964," wilderness areas are defined as being those areas where the nearest road is at least five miles away and where no permanent buildings stand. Activities that could

disrupt native species, such as the use of motorized vehicles is prohibited. More than 100 million acres of land are now preserved as wilderness under this act. Sparsely populated Alaska contains the largest chunk of wilderness areas, over half of it. Although wilderness areas are scattered among most of the lower 48 states, the largest percentage is found in the western states. Few undesignated areas in the contiguous states remain that would qualify as wilderness.

National parks and forests and wildlife refuges can contain wilderness areas. California contains significant wilderness areas, with over 4 million acres of National Forest Wilderness areas, and 1.5 million acres of mostly desert wilderness in the Mojave Desert National Preserve (figure 23.4.*b*).



Figure 23.4.*b*: A variety of unique plant life grows at Mojave Desert National Preserve. Image by John Fowler (CC-BY).

Wilderness areas provide an essential habitat for a wide array of fish, wildlife, and plants, and are particularly important in protecting endangered species. For scientists, wilderness areas serve as natural laboratories, where studies can be performed that would not be possible in developed areas.

National and State Parks

The United States has set aside more land for public recreational use than any other country. The **National Park System** manages more than 380 parks, recreation areas, seashores, trails, monuments, memorials, battlefields, and other historic sites. It consists of more than 80 million acres nationwide (figure 23.4.*c*). The largest national park is Wrangell–St. Elias National Park and Preserve in Alaska with over 13 million acres. California has eight national parks: Channel Islands, Death Valley, Joshua Tree, Lassen, Redwood, Sequoia, Kings Canyon, and Yosemite. Many national parks such as Yosemite, Yellowstone and the Grand Canyon are such popular recreation destinations that the ecosystems of those parks are being severely tested by human activities.



Figure 23.4.*c*: National parks, such as Grand Teton National Park in Wyoming, help conserve biodiversity. (credit: Don DeBold)

Every state has also set aside significant amounts of land for recreational use. The **California State Park System** manages more than one million acres of parklands including: coastal wetlands, estuaries, scenic coastlines, lakes, mountains and desert areas. California's largest state park is Anza-Borrego Desert State Park, which is the largest state park in the United States with 600,000 acres. The stated mission of the California State Park System is "to provide for the health, inspiration and education of the people

of California by helping to preserve the state's extraordinary biological diversity, protecting its most valued natural and cultural resources and creating opportunities for high-quality outdoor recreation".

National Forests

The **National Forest System**, managed by the U.S. Forest Service (part of the United States Department of Agriculture), consists of more than 170 forestlands and grasslands, which are available for activities such as camping, fishing, hiking and hunting. These are managed as multiple use lands, which balance the needs for recreation, grazing, timber, watershed protection, wildlife and fish, and wilderness.

Some examples of national forests are the Sierra National Forest in California and the White Mountain National Forest in New Hampshire. The Coronado National Forest in Arizona is famous for "sky islands", or steep mountain ranges surrounded by low-lying areas. The dramatic increase in elevation is associated with changes in the flora and fauna (figure 23.4.*d*). Explore national forests using this interactive map.



Figure 23.4.*d*: The Santa Teresa Mountains of the Coronado National Forest form "sky islands". Image by Jstuby (public domain).

Wildlife Refuges

The U.S. Fish and Wildlife Service manage more than 500 national **wildlife refuges** (figure 23.4.*e*), which not only protect animal habitats and breeding areas but also provide recreational facilities. Find a Refuge is an interactive map for locating wildlife refuges.



Figure 23.4.*e*: Bobcat at Sonny Bono National Wildlife Refuge in southern California. Image by Mark Stewart/USFWS (public domain).

Supplemental Reading

America's Public Lands Explained. 2016. U.S. Department of the Interior.

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- Multiple Use Lands. 12 May 2015. The United States Department of Justice. Accessed 28 March 2021 (public domain)

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23.5: Ecosystem Restoration

Ecosystem restoration is the process of bringing an area back to its natural state, before it was impacted through destructive human activities. It holds considerable promise as a mechanism for maintaining or restoring biodiversity and reinstating ecosystem services. It requires a broad interdisciplinary approach involving many different scientific fields of study (for example, biology, ecology, hydrology and geology). Reintroducing wolves, a top predator, to Yellowstone National Park in 1995 led to dramatic changes in the ecosystem that increased biodiversity. The wolves (figure 23.5.*a*) function to suppress elk and coyote populations and provide more abundant resources to the detritivores. Reducing elk populations has allowed revegetation of **riparian areas** (those along the banks of a stream or river), which has increased the diversity of species in that ecosystem. Reduction of coyote populations by wolves has increased the prey species previously suppressed by coyotes. In this ecosystem, the wolf is a **keystone species**, meaning a species that is instrumental in maintaining diversity within an ecosystem. Removing a keystone species from an ecological community causes a collapse in diversity. The results from the Yellowstone experiment suggest that restoring a keystone species effectively can have the effect of restoring biodiversity in the community. Ecologists have argued for the identification of keystone species where possible and for focusing protection efforts on these species. It makes sense to return the keystone species to the ecosystems where they have been removed.

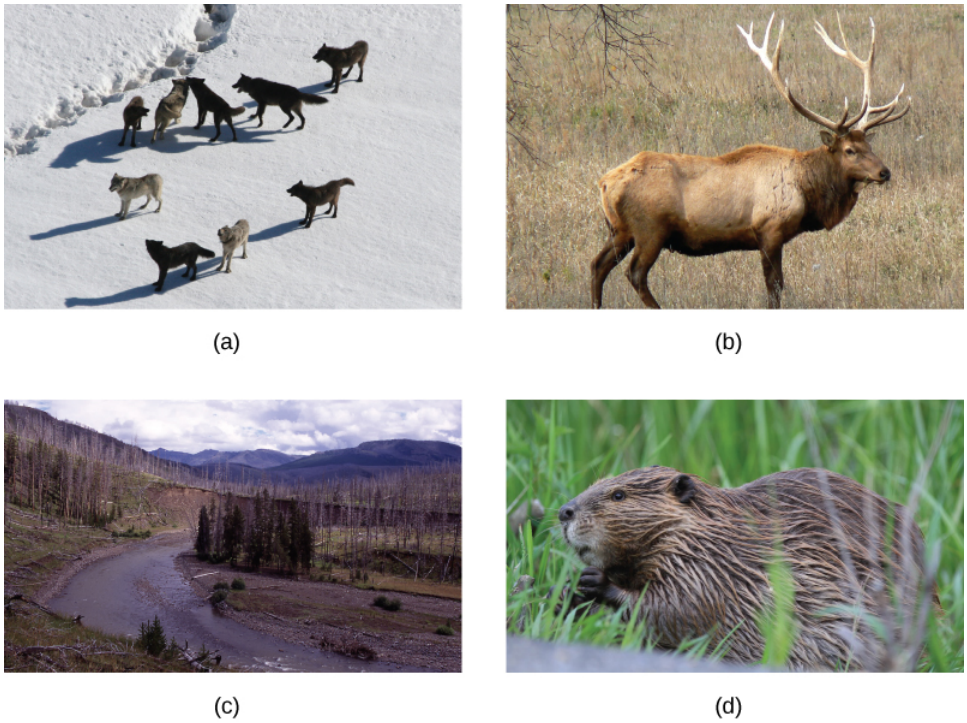


Figure 23.5.*a*: (a) The Gibbon wolf pack in Yellowstone National Park, March 1, 2007, represents a keystone species. The reintroduction of wolves into Yellowstone National Park in 1995 led to a change in the grazing behavior of (b) elk. To avoid predation, the elk no longer grazed exposed stream and riverbeds, such as (c) the Lamar Riverbed in Yellowstone. This allowed willow and cottonwood seedlings to grow. The seedlings decreased erosion and provided shading to the creek, which improved fish habitat. A new colony of (d) beaver may also have benefited from the habitat change. (credit a: modification of work by Doug Smith, NPS; credit c: modification of work by Jim Peaco, NPS; credit d: modification of work by "Shiny Things"/Flickr)

Other large-scale restoration experiments underway involve dam removal. In the United States, since the mid-1980s, many aging dams are being considered for removal rather than replacement because of shifting beliefs about the ecological value of free-flowing rivers. The measured benefits of dam removal include restoration of naturally fluctuating water levels (often the purpose of dams is to reduce variation in river flows), which leads to increased fish diversity and improved water quality (see Dams and Reservoirs for more about the impact of dams). In the Pacific Northwest of the United States, dam removal projects are expected to increase populations of salmon, which is considered a keystone species because it transports nutrients to inland ecosystems during its annual spawning migrations. In other regions, such as the Atlantic coast, dam removal has allowed the return of other spawning anadromous fish species (species that are born in fresh water, live most of their lives in salt water, and return to fresh water to spawn). Some of the largest dam removal projects have occurred recently, such as Elwha Dam on the Olympic Peninsula of

Washington State. The large-scale ecological experiments that these removal projects constitute will provide valuable data for other dam projects slated either for removal or construction.

Besides physical processes, socioeconomic factors must also be considered in a restoration project. Actions of humans have historically been important in shaping ecosystems, and are important in determining the success of restoration efforts. Because the cost to restore an individual site can involve millions of dollars, government support is a necessity.

Environmental Remediation

Danger to human health from both historic and modern pollution requires that cleanup measures be implemented. **Remediation** is aimed at neutralization, containment, and/or removal of the polluting chemicals. The goal is to prevent the spread of the pollution, or to reduce it to levels that will not appreciably risk human health. Many times, it is physically impossible or financially unfeasible to completely clear all contamination. Often, experts and the public disagree on how clean is clean enough.

Many communities are struggling to find the funds and technological expertise needed to clean up polluted areas. Some settings, such as brownfields, can be remediated fairly easily. **Brownfields** are abandoned industrial or commercial facilities or blighted urban areas that need to be cleansed of contamination before they can be redeveloped. Other areas, because of their size or the extreme toxicity of their contaminants, require very expensive, complex, and long-term remediation. Many of these have been designated as Superfund sites.

Superfund sites are areas with the most toxic contamination in the United States. The contamination may not only make the site itself too dangerous to inhabit, but often leaks toxic levels of pollutants into the surrounding soil, water, or air. An example of a Superfund site is Love Canal in Niagara Falls, New York (figure 23.5.*b*). The canal was a chemical waste dump for many years, then in the 1950's was covered with soil and sold to the city. Over time, many homes and a school were built over the former dump. In the 1970's, heavy rains raised the water table and carried contaminants back to the surface. Residents noticed foul smells, and gardens and trees turned black and died. Soon after, rates of birth defects, cancer, and other illnesses began to rise sharply. In 1977, the State of New York and the federal government began remediation work. Buildings were removed, and all residents were bought out and relocated, contaminated deposits and soils were excavated, and remaining soils and groundwater were treated and sealed off to prevent further spread of the contamination. Remediation activities have now been completed at this site.



Figure 23.5.*b*: Love Canal. Source: US Environmental Protection Agency

The type of pollution and the medium affected (air, water, or soil) determine remediation methods. Methods include incineration, absorption onto carbon, chemical methods, or bioremediation. **Bioremediation** is the use of plants, bacteria, or fungus to "digest" the contaminant to a non-toxic or less toxic form. All of these methods tend to be expensive and time-consuming.

Reclamation and Mitigation

Reclamation involves salvaging some features of a degraded habitat, but it may not restore the ecosystem fully (figure 23.5.*c*). For example, instead of abandoning a mined area once resources have been collected, it can be reclaimed by planting vegetation, reshaping the landscape, and redirecting water flow. However the reclaimed land still lacks many features of the original ecosystem, such as complex topography, vegetation that took tens or hundreds of years to grow, soil quality, and an intricate network of streams.

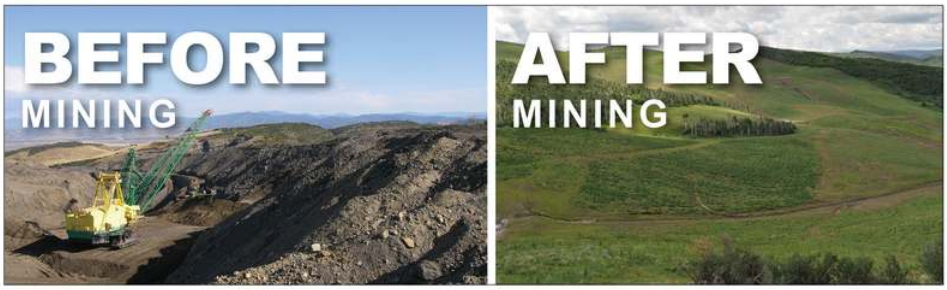


Figure 23.5.*c*: The Seneca Yoast coal once land has been cleared in preparation for mining (left) and after reclamation (right). Image by Peabody Energy, Inc. (CC-BY).

Sometimes, actions can be taken to avoid, reduce or compensate for the effects of environmental damage. Such **mitigation** efforts have been taken by the Army Corps of Engineers during construction projects. The native plants are removed from a site before construction begins and transplanted at a special holding site. After the construction project is completed, the native plants are replanted using those from the holding site. Another example of mitigation might involve the creation or enhancement of wetlands in one area, in order to compensate for permitted wetland losses in another area. Mitigation often goes hand-in-hand with restoration. Texaco, in conjunction with environmental groups and the United States Fish and Wildlife Service, restored 500 acres of agricultural lands in the lower Mississippi Delta to bottomland hardwoods. Texaco received environmental credits for the mitigating effects of the new woodlands on air quality.

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23.6: Economic Influences on Conservation

Economics greatly impacts conservation success. Short-term profits can incentivize individuals, companies, or governments to harvesting resources at an unsustainable rate and at the expense of ecosystem health. In impoverished regions, compromising habitat to grow high-value crops, such as coffee or oil palms, or poaching endangered species may seem like the only source of income. One solution is **debt-for-nature swaps** through which one country forgives the debt of another if the latter agrees to protect natural areas. These conservation efforts can provide a new source of income for residents near the protected areas. For example, the United States forgave $20 million in debt from Costa Rica. In exchange, Costa Rica invested in expanding its protected areas and developing the ecotourism industry, which provides jobs to many of its residents (figure 23.6.a). **Ecotourism** involves visiting and enjoying natural areas while minimizing ecological damage. Ecotourism can benefit local economies and alleviate poverty especially if the earnings from it are reinvested into the communities living near tourist destinations. It generates jobs such as park operators, sellers of local crafts, and tour guides.



Figure 23.6.a: A tourist ziplines over the Costa Rican rainforest. Image by Khaufle at the English language Wikipedia (CC-BY-SA).

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23.7: Individual Choices

Many of the strategies for preserving biodiversity operate at the level of whole governments or large organizations; however, your choices as an individual also play a role in conservation.

Consumer Choices

The products you purchase have differing impacts on biodiversity. Educating yourself on the origin of products and food that you purchase and choosing the sustainable options can help preserve biodiveristy. For example, arabica coffee can be grown in the shade, meaning there is no need to fully clear rainforest vegetation when growing this species (figure 23.7.a). However, robusta coffee requires full sun, and cultivating it has a greater impact or rainforest biodiversity. Monterey Bay Aquarium provides a sustainable seafood guide, which identifies seafood choices that have a lower environmental impact. Choosing local products reduces the amount of fossil fuels that were burned to transport them to you, thus reducing carbon emissions that contribute to climate change.



Figure 23.7.a: Shade-grown coffee at a Columbian farm. Image by Brian Smith/American Bird Conservancy/U.S. Fish and Wildlife Service Northeast Region (CC-BY).

Some products have special certifications that indicate their impact on biodiversity. For example, certified organic products must be cultivated without the use of synthetic pesticides, herbicides, and fertilizers, which pollute the surrounding areas. Additionally, they cannot contain genetically modified organisms (GMOs), which have both positive and negative environmental implications. If you cannot afford to buy all organic produce, see the Environmental Working Group's lists of the Clean Fifteen™ (for which pesticide use is already limited) and Dirty Dozen™ (which are high priority to purchase organic or avoid due to high pesticide residues). The Roundtable on Sustainable Palm Oil (RSPO) certifies oil palm plantations that follow standards such as avoiding deforestation and using fire to clear land. Additionally, RSPO-certified business must follow guidelines to compensate their employees sufficiently. Fair Trade Certified™ goods must meet social and environmental standards that support the United Nation's Sustainable Development Goals.

Resource Conservation

Resource conservation is individual choice that can promote biodiversity. In this case, conservation refers to limiting one's use of resources, such as water, electricity, and gasoline. Landscaping with drought-tolerant plants to limit the need for irrigation or using a low-flow shower head are examples of water conservation. Because much electricity is generated from burning fossil fuels, such as coal and natural gas, conserving electricity reduces carbon emissions associated with climate change. Turning off lights and appliances when not in use and insulating one's home to reduce electricity spent on heating and cooling save money and benefit the environment. Similarly, transportation choices such as carpooling, biking, or taking public transportation can limit carbon emissions. Reusing items or not purchasing unnecessary ones also conserves the energy needed to produce and transport these

goods and reduces plastic waste, which is particularly harmful to aquatic ecosystems. See chapters about Water Resources, Renewable Energy, and Solid Waste Management for more about resource conservation.

Guide to Planting a Pollinator Garden

Whether you have a few feet on your apartment balcony or several acres, you can promote populations of native bees, butterflies, and other pollinators by building a **pollinator garden** (figure 23.7.*b*). The first step is to choose a location. While flowering plants can grow in both shady and sunny locations, consider your audience. Butterflies and other pollinators like to bask in the sun and some of their favorite wildflowers grow best in full or partial sun with some protection from the wind. The next step is to identify your soil type. Take a look at your soil - is it sandy and well-drained or more clay-like and wet? You can turn over a test patch or check out a soil mapper to learn more. Your soil type and the amount of sunlight it gets will help determine the kinds of plants you can grow.



Figure 23.7.*b*: A diversity of plant species support native pollinators in this pollinator garden. Image by Sara "Asher" Morris (CC-BY-NC).

Next, research which varieties of milkweed and wildflowers are native to your area and do well in your soil and sunlight conditions. **Native plants**, those that have historically occurred in the area, are the ideal choice, because they require less maintenance and tend to be heartier. Find a nursery that specializes in native plants near you - they'll be familiar with plants that are meant to thrive in your region. Some examples of pollinator-friendly plants native to California, include the California poppy, California lilac, milkweed, and foothill penstemon. The California Native Plant Society and UC Berkeley Urban Bee Lab have additional plant suggestions. It's essential to choose plants that have not been treated with pesticides. Choosing **perennials** will ensure your plants come back each year, reducing the need for maintenance.

Remember to think about more than just the summer growing season. Pollinators need nectar early in the spring, throughout the summer and even into the fall. Choosing plants that bloom at different times will help you create a bright and colorful garden that both you and pollinators will love for months!

Some native bee species use bare soil for nesting. While applying mulch can help control weeds, leaves some bare soil if possible. Some native pollinators also nest in tiny cavities, which may already occur naturally in or near your garden or can be provided with bee boxes.

Make sure to weed and water your garden to keep it healthy. It may take some time, but you will eventually see butterflies and other pollinators enjoying your garden.

Modified by Melissa Ha from the U.S. Fish and Wildlife Service (public domain).

Citizen Science

Finally, citizen science provides the opportunity to be directly involved in biological conservation efforts. For some opportunities like Globe at Night, which assess light pollution, or the Lost Ladybug Project, data can be collected independently

and submitted online. Others, like bird banding, are scheduled events in which experts train a group of volunteers to complete fieldwork (figure 23.7.*c*). The federal government's citizen science database lists many such opportunities.



Figure 23.7.*c*: Left: Students returning from taking phenology measurements on native trees in a native forest conservation area on Hawaii Island. Phenology refers to the timing of events in an organism's life cycle. Right: Americorp members preparing ʻōhiʻa tree cuttings for rooting and propagation – with plants to be used for disease resistance screening. Left image by UFS/USDA (public domain). Right image by USFS (public domain).

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CHAPTER OVERVIEW

Chapter 24: Human Global Environment

24.1: Introduction to Climate Change

24.2: Anthropogenic Climate Change

24.3: Current and Future Climate Change Impacts

24.4: Climate Strategies

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24.1: Introduction to Climate Change

Introduction to Climate Change

- Please read and watch the following Learning Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 1 hour.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Define global climate change
- Summarize the effects of the Industrial Revolution on global atmospheric carbon dioxide concentration
- Describe three natural factors affecting long-term global climate
- List two or more greenhouse gases and describe their role in the greenhouse effect

Introduction

All biomes are universally affected by global conditions, such as climate, that ultimately shape each biome's environment. Scientists who study climate have noted a series of marked changes that have become increasingly evident during the last sixty years. **Climate change** refers to the complete set of climate characteristics—temperature; precipitation; pressure systems; wind patterns; and oceanic currents—that are changing locally, regionally, and globally due to human influences. It is closely related to **global warming**, also called global heating, which describes the general trend of increasing global temperatures we see under climate change. However, *climate change* is more inclusive of the totality of abiotic effects of a warming planet.

Climate and Weather

A common misconception about global climate change is that a specific weather event occurring in a particular region (for example, a very cool week in June in central Saskatchewan) is evidence of global climate change. However, a cold week in June is a weather-related event and not a climate-related one. These misconceptions often arise because of confusion over the terms climate and weather.

Video



Discover the real reason we confuse weather and climate in this 5-minute video from Hot Mess (US PBS). Question after watching: How does our personal experience of weather have an effect on how we view climate change?

Climate refers to the long-term, predictable atmospheric conditions of a specific area. The climate of a biome is characterized by having consistent temperature and annual rainfall ranges. Climate does not address the amount of rain that fell on one particular day in a biome or the colder-than-average temperatures that occurred one season. In contrast, **weather** refers to the conditions of the atmosphere during a short period of time. Weather forecasts are usually made for 48-hour cycles. Long-range weather forecasts are available but can be unreliable.

To better understand the difference between climate and weather, imagine that you are planning an outdoor event in Kamloops, BC. You would be thinking about *climate* when you plan the event in the summer rather than the winter because you have long-term knowledge that any Saturday in May through August would be a better choice for an outdoor event in Kamloops than a Saturday in January. However, you cannot determine the specific day on which that event should be held because it is difficult to accurately predict the weather. Climate can be considered "average" weather.

? Optional Activity 24.1.1

Which of the following is an example of climate?

A. An intense thunderstorm in Houston.
B. The average temperature in Chicago over the past 50 years.
C. An unusually hot fall in Boston.
D. A foggy day in San Francisco.

Answer

B. The average temperature in Chicago over the past 50 years.

Global Climate Change

Climate change can be understood by approaching three areas of study:

- current and past global climate change
- causes of past and present-day global climate change
- ancient and current results of climate change

It is helpful to keep these three different aspects of climate change clearly separated when consuming media reports about global climate change. It is common for reports and discussions about global climate change to confuse the data showing that Earth's climate is changing with the factors that drive this climate change.

Evidence for Past and Current Global Climate Change

Since scientists cannot go back in time to directly measure climatic variables, such as average temperature and precipitation, they must instead indirectly measure temperature. To do this, scientists rely on historical evidence of Earth's past climate.

Antarctic ice cores are a key example of such evidence. These **ice cores** are samples of polar ice obtained by means of drills that reach thousands of meters into ice sheets or high mountain glaciers. Viewing the ice cores is like traveling backwards through time; the deeper the sample, the earlier the time period. Trapped within the ice are bubbles of air and other biological evidence that can reveal temperature and carbon dioxide data. Antarctic ice cores have been collected and analyzed to indirectly estimate the temperature of the Earth over the past 400,000 years (Figure 24.1.1a). The 0°C on this graph refers to the long-term, modern-day average. Temperatures that are greater than 0°C exceed Earth's long-term average temperature. Conversely, temperatures that are less than 0°C are less than Earth's average temperature. This figure shows that there have been periodic cycles of increasing and decreasing temperature.

Before the late 1800s, the Earth was as much as 9°C cooler and as much as 3°C warmer. Most of the past 400,000 years have been colder than today. Most of the past warming and cooling periods happened over long enough time scales that the majority of organisms were able to adapt and evolve with the changing climate.

The graph in Figure 24.1.1b shows that the atmospheric concentration of carbon dioxide has also risen and fallen in periodic cycles. Note the relationship between carbon dioxide concentration and temperature. Figure 24.1.1b shows that carbon dioxide levels in the

atmosphere have historically cycled between 180 and 300 parts per million (ppm) by volume.

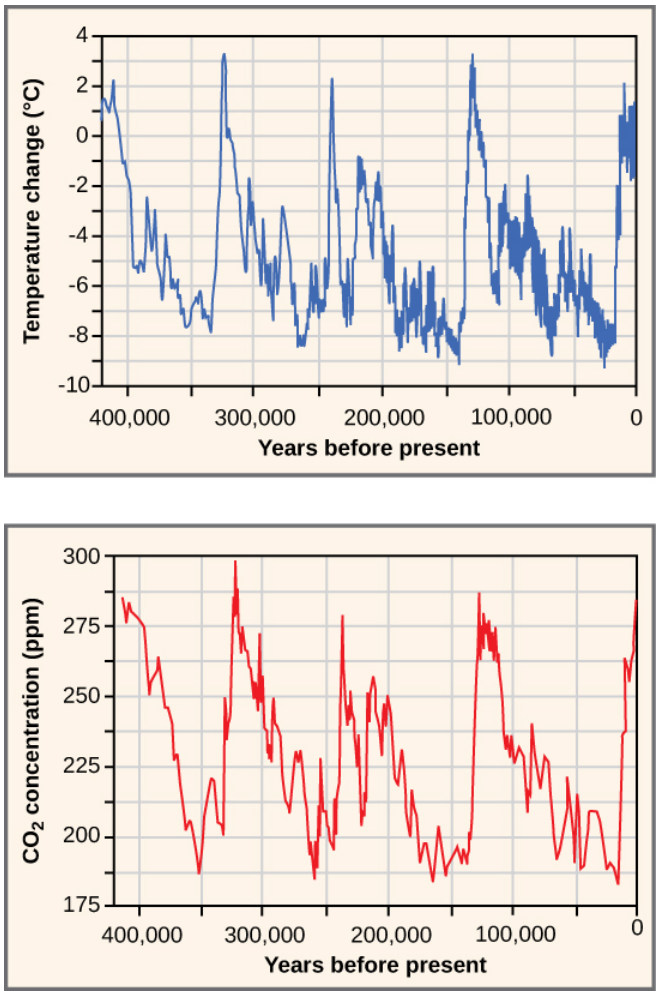


Figure 24.1.1**:** Ice at the Russian Vostok station in East Antarctica was laid down over the course of 420,000 years and reached a depth of over 3,000 m. By measuring the amount of CO_2 trapped in the ice, scientists have determined past atmospheric CO_2 concentrations. Temperatures relative to modern-day were determined from the amount of deuterium (an isotope of hydrogen) present.

Figure 24.1.1 does not show the last 2,000 years with enough detail to compare the changes in Earth's temperature during the last 400,000 years with the temperature change that has occurred in the more recent past. Three significant temperature anomalies, or irregularities, have occurred in the last 2000 years. The first two are the Medieval Climate Anomaly (or the Medieval Warm Period) and the Little Ice Age. A third temperature anomaly aligns with the Industrial Era.

The **Medieval Climate Anomaly** occurred between 900 and 1300 AD. During this time period, many climate scientists think that slightly warmer weather conditions prevailed in many parts of the world; the higher-than-average temperature changes varied between 0.10 °C and 0.20 °C above the norm. Although 0.10 °C does not seem large enough to produce any noticeable change, it did free seas of ice. Remember, the temperatures stated here are global averages. Some areas became much warmer, especially at higher latitudes, and some areas remained at their same averages. Because of the warming in the higher latitudes, the Vikings were able to colonize Greenland.

The **Little Ice Age** was a cold period that occurred between 1550 AD and 1850 AD. During this time, a slight cooling of a little less than 1°C was observed in North America, Europe, and possibly other areas of the Earth. This 1°C change in global temperature is a seemingly small deviation in temperature (as was observed during the Medieval Climate Anomaly); however, it also resulted in noticeable changes. Historical accounts reveal a time of exceptionally harsh winters with much snow and frost.

The **Industrial Revolution**, which began around 1750, was characterized by changes in much of human society. Advances in agriculture increased the food supply, which improved the standard of living for people in Europe and North America. New

technologies were invented and provided jobs and cheaper goods. These new technologies were powered using fossil fuels, especially coal. The Industrial Revolution starting in the early nineteenth century ushered in the beginning of the Industrial Era. When a **fossil fuel** (coal, oil, or natural gas) is burned, carbon dioxide is released. With the beginning of the Industrial Era, atmospheric carbon dioxide began to rise (Figure 24.1.2).

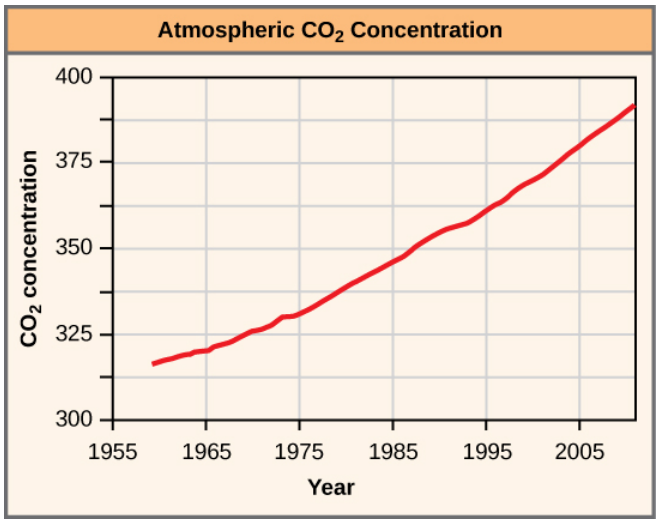


Figure 24.1.2: The atmospheric concentration of CO_2 has risen steadily since the beginning of industrialization, which began in 1750. Modern isotopic measurements of atmospheric CO_2 began in the late 1950s, which is reflected in this graph.

Causes of Past Climate Change

Since it is not possible to go back in time to directly observe and measure climate, scientists use indirect evidence to determine the **drivers**, or causes, that may be responsible for climate change. The indirect evidence includes data collected using ice cores, boreholes (a narrow shaft bored into the ground), tree rings, glacier lengths, pollen remains, and ocean sediments. The data shows a correlation between the timing of temperature changes and drivers of climate change: before the Industrial Era (pre-1780), there were three drivers of climate change that were not related to human activity or atmospheric gases.

The first of these is the **Milankovitch cycles**. The Milankovitch cycles describe the effects of slight changes in the Earth's orbit on Earth's climate. The length of the Milankovitch cycles ranges between 19,000 and 100,000 years. In other words, one could expect to see some predictable changes in the Earth's climate associated with changes in the Earth's orbit at a minimum of every 19,000 years and maximum every 100,000 years.

The variation in the sun's intensity is the second natural factor responsible for climate change. **Solar intensity** is the amount of solar power or energy the sun emits in a given amount of time. There is a direct relationship between solar intensity and temperature. As solar intensity increases (or decreases), the Earth's temperature correspondingly increases (or decreases). Changes in solar intensity have been proposed as one of several possible explanations for the Little Ice Age.

Finally, volcanic eruptions are a third natural driver of climate change. Volcanic eruptions can last a few days, but the solids and gases released during an eruption can influence the climate over a period of a few years, causing short-term climate changes. The gases and solids released by volcanic eruptions can include carbon dioxide, water vapor, sulfur dioxide, hydrogen sulfide, hydrogen, and carbon monoxide. Generally, volcanic eruptions cool the climate. This occurred in 1783 when volcanoes in Iceland erupted and caused the release of large volumes of sulfuric oxide. This led to **haze-effect cooling**, a global phenomenon that occurs when dust, ash, or other suspended particles block out sunlight and trigger lower global temperatures as a result; haze-effect cooling usually extends for one or more years. In Europe and North America, haze-effect cooling produced some of the lowest average winter temperatures on record in 1783 and 1784.

However, today, greenhouse gases are probably the most significant drivers of the climate. When heat energy from the sun strikes the Earth, gases known as **greenhouse gases** trap the heat in the atmosphere, just as the glass panes of a greenhouse keep heat from escaping. The greenhouse gases that affect Earth include carbon dioxide, methane, water vapor, nitrous oxide, and chlorofluorocarbons (CFCs). Approximately half of the radiation from the sun passes through these gases in the atmosphere and strikes the Earth. This radiation is converted into thermal radiation on the Earth's surface, and then a portion of that energy is re-

radiated back into the atmosphere. Greenhouse gases, however, reflect much of the thermal energy back to the Earth's surface. The more greenhouse gases there are in the atmosphere, the more thermal energy is reflected back to the Earth's surface. Greenhouse gases absorb and emit radiation and are an important factor in the greenhouse effect: the warming of Earth due to carbon dioxide and other greenhouse gases in the atmosphere.

Video



Discover the intricacies of Earth's greenhouse effect in this 3-minute video.
Question after watching: How do the so-called greenhouse gases act to insulate the Earth? Why do more greenhouse gases lead to a warmer planet?

Optional Activity 24.1.2

What is the greenhouse effect?

A. Certain gases in the atmosphere trap heat and warm the Earth
B. Life on Earth 'exhales' gas that warms up the atmosphere
C. The tilt of the Earth changes the amount of solar energy the Earth receives
D. The Sun is putting out more radiant energy over time

Answer

A. Certain gases in the atmosphere trap heat and warm the Earth.

Results of Past Climate Change

Climate change is not a new phenomenon. Scientists have geological evidence of the consequences of long-ago climate change. Increased global temperatures and greenhouse gases have been associated with at least one planet-wide extinction event during the geological past. The Permian extinction event occurred about 251 million years ago toward the end of the roughly 50-million-year-long geological time span known as the Permian period. This geologic time period was one of the three warmest periods in Earth's geologic history. Scientists estimate that more than 90 percent of all life became extinct near the end of the Permian period. Organisms that had adapted to wet and warm climatic conditions, such as annual rainfall of 300–400 cm and 20 °C–30 °C in the tropical wet forest, may not have been able to survive the Permian climate change.

During the past 2 million years, there have been at least 10 cycles of natural warming and cooling on a planetary scale. When the polar ice caps melted during warming periods, sea levels rose to well above their earlier levels, and a larger portion of Earth experienced tropical climates. During cooling periods, the polar ice caps expanded, sea levels dropped, and tropical species' ranges contracted. Sometimes these changes occurred gradually, which enabled the affected species to adapt. But the onset of some climate change periods was abrupt, causing major ecosystem disruptions and global mass extinction events. Yet, nature recovered every time; many of the species we see today are survivors of previous climate change events. It is thus fair to ask why today's climate change is of such concern to us.

Video



A look at the history of climate change on Earth can give us some much-needed perspective on our current climate dilemma because, the surprising truth is, what we are experiencing now is different than anything this planet has encountered before. This 11-minute video gives an overview of Earth's prior climates.
Question after watching: In what way is the current climate change different than historical climate changes?

Climate Change's Impact on Humans (Past and Present)

History provides us with many lessons to illustrate the impact of climate change on human societies. These lessons start with the earliest well-documented example of a societal collapse—that of the Middle East's Natufian communities roughly 10,000 years ago—which has been attributed to climatic changes. Since then, climate change has regularly contributed to the collapse of complex human societies across the world. Notable examples of such collapses include the Akkadian Empire (the world's first empire) of the Middle East, Egypt's Old Kingdom (the builders of the pyramids), Central America's Classic Mayan civilization, the first English colony in America, several Chinese dynasties, and the Late Bronze Age societies along the Mediterranean Sea. Also, in Southern Africa, the fall of the Mapungubwe Kingdom has been attributed to crop failures and declining grazing lands due to regional droughts and warming cycles.

Similar patterns hold true today, only on a global scale. Because of humans' collective lack of response in addressing the drivers of climate change, more people will suffer the consequences than will not. Prominently, many parts of the world are already seeing higher temperatures and longer droughts. These conditions are compromising our quality of life by leading to more intense wildfires, increased incidences of vector-borne disease, increased crop failures, and increased competition for water. Many coastal areas are also seeing storms increasing in intensity and frequency, exposing people living near large rivers, deltas, and estuaries to more frequent flooding and storm surges. For example, the impacts from Cyclone Idai, one of the worst storms on record to have hit Africa, led to the deaths of more than 1,000 people (Figure 24.1.3). While no single flooding event can be attributed to climate change, it is undeniable that warmer oceans create conditions for hurricanes and cyclones to be stronger, bigger, and more frequent. Sea level rise is expected to leave many low-lying oceanic islands uninhabitable within a few decades. With all these impacts expected to increase the competition for space under an increasing human population, it would be wise for the world's governments to start preparing for millions of climate refugees that need to be relocated soon.

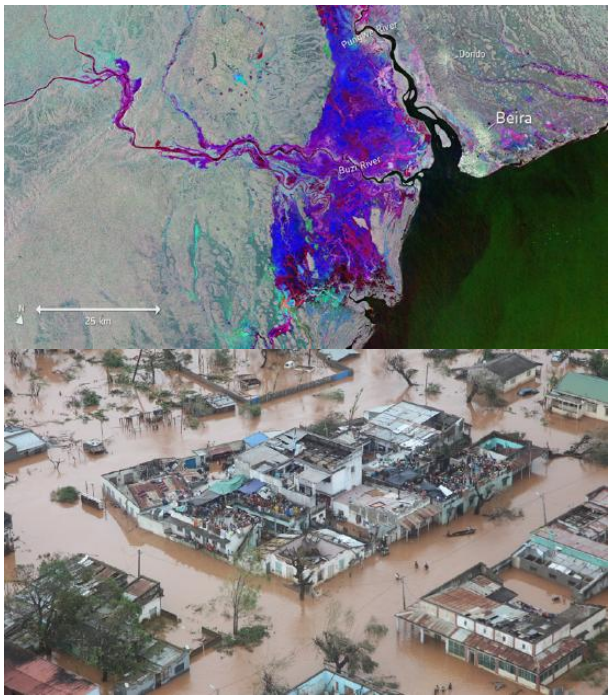


Figure 24.1.3: (Top) A Copernicus Sentinel-1 satellite image showing the extent of flooding (areas shown in blue) in central Mozambique after Cyclone Idai made landfall on 15 March, 2019. Photograph by European Space Agency, https://www.flickr.com/photos/europeanspaceagency/47477652401, CC BY-SA 2.0. (Bottom) People in Beira, Mozambique, taking refuge on rooftops to escape flooding brought by Cyclone Idai. Photograph by World Vision, https://www.flickr.com/photos/dfid/46570320385, CC BY 2.0.

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- **44.5: Climate and the Effects of Global Climate Change** by OpenStax is licensed CC BY 4.0.

24.2: Anthropogenic Climate Change

Anthropogenic Climate Change

- Please read and watch the following Learning Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 2 hours.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

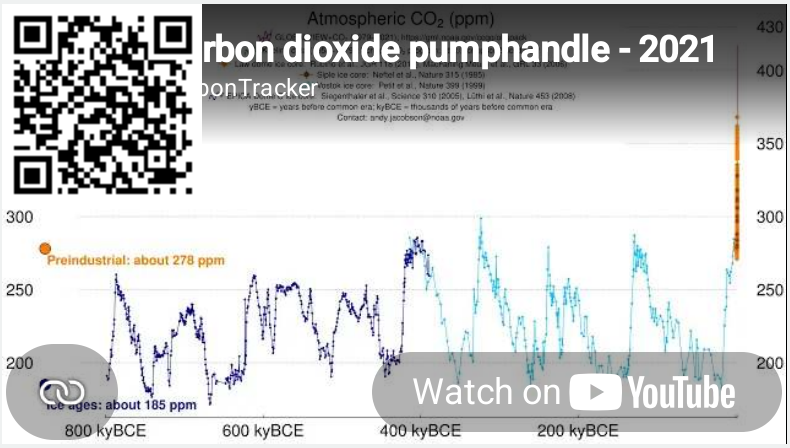
Learning Objectives

- Identify the historical beginnings of anthropogenic climate change
- Explain how current climate change is measured
- Describe the scientific consensus on anthropogenic climate change
- Identify human impacts on specific greenhouse gases

Introduction

Evidence supports the relationship between atmospheric concentrations of carbon dioxide and temperature: as carbon dioxide rises global temperature rises. Since 1950, the concentration of atmospheric carbon dioxide has increased from about 280 ppm to 382 ppm in 2006. In 2021, the atmospheric carbon dioxide concentration was 415 ppm.

Video



This 2.5-minute video shows how atmospheric CO_2 has varied recently and also over the last 800,000 years as determined by many CO_2 monitoring stations (shown on the insert map). It is also instructive to watch the CO_2 variation of the video by latitude. This shows that most of the sources of CO_2 are in the Northern Hemisphere where humans reside.

Question after watching: What general trends do you notice over the last 800,000 years? How is the current climate breaking those trends?

Scientists look at patterns in data and try to explain differences or deviations from these patterns. The atmospheric carbon dioxide data reveal a geologic pattern of carbon dioxide increasing and decreasing, cycling between a low of 180 ppm and a high of 300 ppm before decreasing again, generally over 100,000 year Malankovich cycles (see Unit 5.3.1). Scientists have concluded that it took around 50,000 years for the atmospheric carbon dioxide level to increase from its traditionally low minimum concentration at the height of the last ice age to its higher maximum concentration. However, starting recently, atmospheric carbon dioxide concentrations have increased beyond the historical maximum of 300 ppm. The current increases in atmospheric carbon dioxide

have happened very quickly—in a matter of hundreds of years rather than thousands of years. What is the reason for this difference in the rate of change and the amount of increase in carbon dioxide and other greenhouse gases (GHGs)?

Anthropogenic Climate Change

Anthropogenic climate change refers to the impacts of humans on the climate system. Scientists generally look to the Industrial Era as the beginning of anthropogenic climate change, which is the advent of the use of fossil fuels, beginning with coal, to power machinery in the middle of the 1700s. Some climate scientists argue that anthropogenic climate change actually begins much earlier than the Industrial Era and that humans began impacting the climate through deforestation and land clearing to grow food. This would include farming grains in Europe and the Middle East during the first Agricultural Revolution around 8,000 years BCE and developing artificial wetlands for rice cultivation in Asia around 5,000 years BCE. Clearing vegetation for crops is a type of **climate-forcing**, meaning greenhouse gases (in this case, carbon dioxide) are being released into the atmosphere. The carbon dioxide storage capacity of crops is generally lower than that of the forests originally there. Creating wetlands is also a carbon source due to the bacterial decay of organic matter within wetlands that produces methane.

In fact, whether anthropogenic climate change started with the Agricultural Revolution or the Industrial Revolution is not important, because the really significant climate changes did not start until the early part of the 20th century. Human activities and population size are intertwined. As more and more of the world's population adopts a resource-intensive lifestyle, the climate problem becomes worse. These lifestyles currently require fossil fuels, which provide relatively cheap and abundant energy and are used for everything from transportation and heating and cooling to industry and food production.

This escalating level of industrialization and mechanization of our lives has driven the anthropogenic climate change of the past century. The trend of mean global temperatures since 1880 is shown in Figure 24.2.1. For approximately the past 55 years, the temperature has increased at a relatively steady and rapid rate, especially compared to past changes. The average temperature now is approximately 1.0°C higher than before industrialization, and two-thirds of this warming has occurred since 1975. Since 1880, average global surface temperatures have trended upward and most of that warming has occurred since 1970. Since the ocean is absorbing a lot of the additional trapped heat, surface temperatures include both land surface and ocean temperatures.

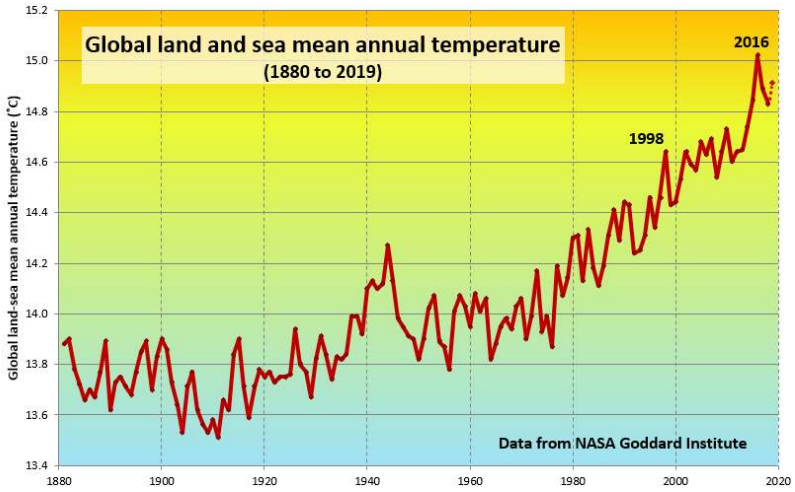


Figure 24.2.1: Global mean annual temperatures for the period from 1880 to 2019. The value for 2019 is projected, based on only 6 months of data. 1998 and 2016 were strong El Niño years. © Steven Earle. CC BY. Based on data from NASA.

Video



This 60-second animation from two of the world's leading science academies brings you the science behind climate change.

Question after watching: Of the graphs shown, which had you seen before (similar or the same)? Which ones were new to you? What does this make you think about?

Optional Activity 24.2.1

How has the global average temperature changed since the Industrial Revolution?

A. Cooler by 0.1°C
B. The temperature has gone up and down, but remains overall the same
C. Warmer by more than 1°C
D. Warmer by almost 2°C

Answer

C. Warmer by more than 1°C

How Do We Know? Measuring Current Climate Change

Changes in land surface or ocean surface temperatures can be expressed as temperature **anomalies**. A temperature anomaly is a difference in average temperature measurement from a predetermined datum (or baseline). This datum is the average temperature of a particular date range, for example, 1951 to 1980. Another common datum is the last century (1900-2000). Therefore, an anomaly of 1.25 ℃ for 2015 (last century datum) means that the average temperature for 2015 was 1.25 ℃ greater than the 1900-2000 average. In 1950, the temperature anomaly was -0.28 ℃, so this is -0.28 ℃ lower than the 1900-2000 average [3]. These temperatures are annual average surface temperatures. Figure 24.2.2 shows the global mean temperature estimates for the period of 1880 to 2020 using the datum of the 1951-1980 average temperature.

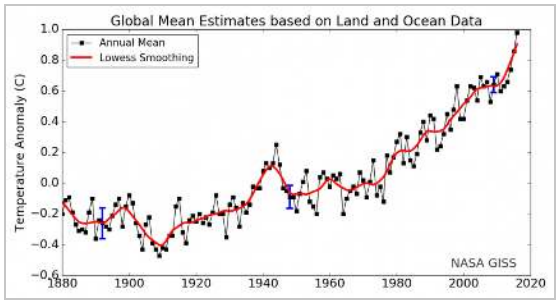


Figure 24.2.2: Land-ocean temperature index, 1880 to present, with a base time 1951-1980. The solid black line is the global annual mean and the solid red line is the five-year lowess smooth curve. The blue uncertainty bars (95% confidence limit) account only for incomplete spatial sampling.
[From https://opengeology.org/textbook/15-...limate-change/ Adapted from *Source: National Climate Data Center*]

Other valuable insights have been obtained by running sophisticated mathematical global **climate models** on high-powered supercomputers. These "virtual experiments" examine the potential climatic responses to increases in atmospheric CO_2. These computer simulations are known as three-dimensional general circulation models (GCMs). The models simulate the complex movements of energy and mass in the global circulation of the atmosphere. They also examine the interactions of these processes with physical variables that are important aspects of climate, such as temperature and precipitation. A strong tendency that emerges from these virtual experiments is that global warming and associated climate changes are a likely consequence of the well-documented increases of CO_2 and other GHGs in the atmosphere.

Many such simulation experiments have examined the scenario of a doubling of CO_2 concentration to 800 ppm from its recent concentration of just over 400 ppm. These experiments suggest that such a doubling would result in an increase of 1°C to 4°C in the average temperature of the surface atmosphere. The intensity of warming is predicted to be greatest in high-latitude regions, where the temperature increases might be two to three times greater than in the tropics.

Warming of the lower atmosphere will be one likely change that will be caused by an increased intensity of the greenhouse effect. However, there could also be important effects that occur indirectly due to increased temperatures. The most important of these would include large-scale shifts in the patterns of atmospheric circulation. Such shifts would likely result in changes in the amounts, distribution, and seasonality of precipitation. Changes in precipitation regimes would influence soil moisture, which would greatly affect the distribution and productivity of vegetation, both natural and managed. These changes in precipitation regime would likely have much greater effects on agricultural and wild ecosystems than would any direct influence of a warmed atmosphere.

Indigenous Connections: Monitoring Climate Change

"Indigenous research methodologies are "…as old as our ceremonies and our nations. They are with us and have always been with us" (Cardinel, 2001). The methodologies for Indigenous-led research are varied across and within First Nation, Inuit, and Métis communities across Canada reflecting the diversity of worldviews and ways of knowing" (First Peoples Group, 2022).

"Many Indigenous climate monitoring projects co-apply Indigenous Knowledge Systems with science bringing together the strengths of both knowledge systems. This has been described as two-eyed seeing (Etuaptmumk in Mi'kmaw), which involves 'learning to see from one eye with the strengths of Indigenous Knowledges and ways of knowing, and from the other eye with the strengths of mainstream knowledges and ways of knowing, and to use both these eyes together, for the benefit of all' (Marshall, 2020)" (First Peoples Group, 2022).

"Indicators are used by many Indigenous Peoples to understand and communicate about ecological change. They are the signs and signals that have guided understanding and decisions within Indigenous communities for hundreds if not thousands of years. Climate indicators can relate to:

- radiation (solar radiation or sunlight; surface temperature and thermal radiation)
- the atmosphere (e.g., temperature, precipitation, wind, humidity);
- the land (e.g., changes in permafrost, soil moisture, soil temperature, water-table depth)
- water quantity (e.g., flow, water depth) or quality (e.g., pH, dissolved oxygen, nitrate, phosphates, water temperature)
- ice and snow (e.g., timing of ice formation and breakup, thickness, quality; snow depth)

- plants and animals (e.g., timing of arrival of species, species population and distribution, health and body condition, taste and yield of berries, spectroscopy)" (First Peoples Group, 2022).

"Elders and Knowledge keepers hold invaluable knowledge about the changes to the land and the environment as a whole. Going out on the land with Knowledge holders can provide a natural space for intergenerational knowledge transfer and Indigenous Knowledge sharing. Participatory video is a newer method of documenting community climate observations and stories through mobilizing stories and collectively-held knowledge with diverse audiences to inform climate adaptation" (First Peoples Group, 2022).

"Many Indigenous climate monitoring projects also follow scientific methods for collecting data. Many monitoring projects incorporate sensors and automated instrumentation which remain in the field such as weather stations, hydrological sensors, trail cameras, soil temperature sensors, etc. Some community-based monitoring projects are even using observations from space-based remote sensors (e.g., Landsat 8, LIDAR)" (First Peoples Group, 2022).

In 2022, the federal government announced $800 million towards Indigenous-led conservation efforts, including those that help to mitigate climate change, like the BC Northern Shelf Bioregion: https://pm.gc.ca/en/news/news-releases/2022/12/07/protecting-more-nature-partnership-indigenous-peoples

Sources:

Cardinel, L. 2001. What is an Indigenous Perspective? Canadian Journal of Native Education, 25(2), 180-182.

Elder Dr. Albert Marshall from Reid, Andrea J Lauren E. Eckert, John-Francis Lane, Nathan Young, Scott G. Hinch, Chris T. Darimont, Steven J. Cooke, Natalie C. Ban, Albert Marshall. 2020. “Two-Eyed Seeing”: An Indigenous framework to transform fisheries research and management. Fish and Fisheries 22:2, p243-261. Available at: https://doi.org/10.1111/faf.12516



This beautifully illustrated animation video explains what climate change means for Tsay Keh Dene, the changes that elders have observed in their territories of British Columbia, and how these changes will impact local cultures and traditional practices. It describes the Tsay Keh Dene and Carcross Tagish Community-Based Climate Monitoring project funded by Crown-Indigenous Relations and Northern Affairs Canada.

Scientific Consensus: Global Anthropogenic Climate Change is Real

The **Intergovernmental Panel on Climate Change** (IPCC)—established by the United Nations Environment Programme and the World Meteorological Organization in 1988—is responsible for reviewing the scientific literature on climate change and issuing periodic reports on several topics, including the scientific basis for understanding climate change, our vulnerability to observed and predicted climate changes, and what we can do to limit climate change and minimize its impacts. The IPCC uses this information to evaluate current impacts and future risks, in addition to providing policymakers with assessments. These assessments are released about once every six years. The Panel is on their most recent Synthesis Report, the 6th Assessment Report. Working group reports were released in 2021-2022. Hundreds of leading scientists from around the world are chosen to author these reports. Over the

history of the IPCC, these scientists have reviewed thousands of peer-reviewed, publicly available studies. The scientific consensus according to the last IPCC assessment is clear: global climate change is real and humans are very likely the cause for this change.

Additionally, the major scientific agencies of Canada and the Canadian government also agree that climate change is occurring and that humans are driving it. From the Environment and Climate Change Canada: “Human activity is the main cause of climate change. Carbon dioxide is the main cause of human-induced climate change.” Many independent scientific organizations have released similar statements, both in Canada and abroad. This does not necessarily mean that every scientist agrees on the strength of each component of the climate change system, but nearly universal agreement exists that climate change is happening and is primarily caused by excess greenhouse gases from human activities.

Video



This 14-minute video from the IPCC summarizes much of the 6th Assessment Report on Impacts, Adaptation, and Vulnerability with a global focus.
Question after watching:

Climate varies naturally over a wide range of time scales. In general, climate changes prior to the Industrial Revolution in the 1700s can be explained by natural causes, such as changes in solar energy, volcanic eruptions, and natural changes in greenhouse gas (GHG) concentrations. Recent changes in climate**,** however, cannot be explained by natural causes alone. Research indicates that natural causes are very unlikely to explain most observed warming, especially warming since the mid-20th century. Rather, human activities, especially our combustion of fossil fuels, explains the current warming (Figure 24.2.3). The scientific consensus is clear: through alterations of the carbon cycle, humans are changing the global climate by increasing the effects of something known as the greenhouse effect.

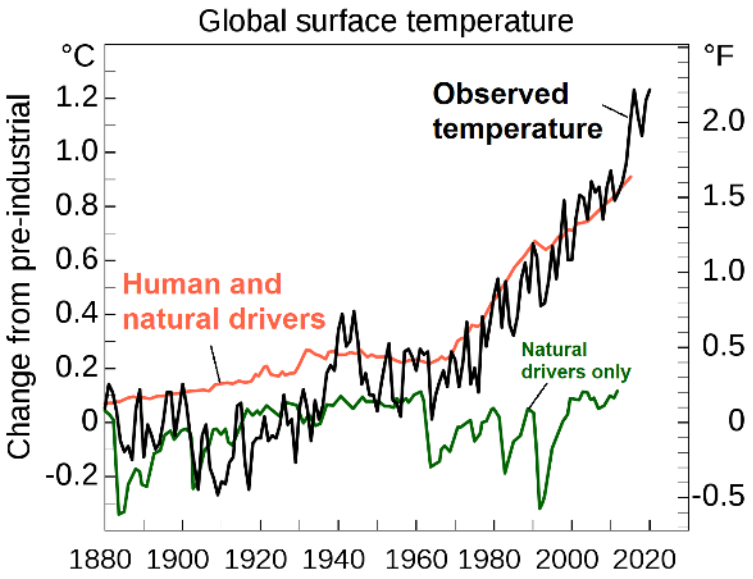


Figure 24.2.3: This graph shows the predicted temperatures from two climate models and observed temperatures from 1880 to 2020. The first model considered only natural factors that could influence temperature and is represented by the green line (bottom). It shows some fluctuations in temperature by no overall increase or decrease. The second model considered both human and natural factors and is represented by the orange line (top). It shows an overall increase in temperature. Actual observations (black, jagged line; middle) more closely match the second model. Overall, temperature has increased about 1.2°C since pre-industrial times. Image relabeled from Efbrazil CC-BY-SA.

Climate change forecasting is famously complex, with a great amount of uncertainty attached to the task. The general models used for climate change forecasting need to account for a great number of highly variable components, each affecting one another across the only planet we can adequately measure or examine (we have no other planet where we can test predictions). Among thousands of considerations, **climatologists**, scientists who study climate, need to account for how human activities might change over time, and how these activities will change the atmosphere's composition. They also need to account for how much CO_2 the world's oceans and plants will absorb, and how wind and fire might influence these processes. Combining all the component parts, climatologists then need to estimate how increased temperatures will affect the polar ice caps, how the melting ice will affect oceanic conditions and currents which, in turn, will affect terrestrial conditions and weather patterns. Uncertainty also exists over interactive effects of some drivers. For example, higher temperatures increase evaporation and cloud cover which, in turn, will have a moderate cooling effect. Because of the complexity of these and other variables going into climate models, a great number of research groups are encouraged to develop their own climate forecasts, each using a range of different scenarios on how human activity might change in the future.

By regularly doing extensive reviews of all the evidence and climate science literature, the IPCC has found that, despite the complexity of climate models, results of all the models taken together exhibited significant agreement with changes already observed. Climate change models have also proven reliable in predicting responses of biodiversity to climate change. While climatologists continue to improve on the finer details of their models, conservation biologists can and should confidently use the climate forecasts available for general conservation planning purposes.

Specific Human Impacts on Greenhouse Gases

Recall that GHGs are probably the most significant drivers of current climate change. The GHGs that affect Earth include carbon dioxide, methane, water vapor, nitrous oxide, and ozone. Water vapor is the most abundant greenhouse gas and also the most important in terms of its contribution to the natural greenhouse effect, despite having a short atmospheric lifetime. Some human activities can influence local water vapor levels. However, on a global scale, the concentration of water vapor is controlled by temperature, which influences overall rates of evaporation and precipitation. Therefore, the global concentration of water vapor is not substantially affected by direct human emissions.



Figure 24.2.6: The burning of fossil fuels in industry and by vehicles releases carbon dioxide and other greenhouse gases into the atmosphere. (CC-BY-SA 4.0 “Pöllö”/Wikimedia Commons)

Sinks and Sources

Places in the ecosystem that store GHGs are reservoirs. Places that supply and remove are **sources** and **sinks**, respectively. If more GHGs are released than stored, the place is a source. If more GHGs are absorbed than emitted, the reservoir is a sink. A reservoir can change from a sink to a source and vice versa. For example, a forest is a sink for carbon, but when the forest burns it becomes a carbon source.

Carbon Dioxide

Carbon dioxide (CO_2) is the primary greenhouse gas that is contributing to recent global climate change. Healthy living forests and the oceans act as carbon sinks. The mantle is a natural source of carbon from volcanic gases. The link between human-induced climate change and atmospheric CO_2 concentrations was first highlighted in the late 19th century by Arrhenius. However, it was not until the mid-1950s that scientists started to raise concerns about increasing CO_2 concentrations in the atmosphere. By the 1980s, as global annual mean temperatures started to rise, consensus about climate change linked to CO_2 began to spread among the broader public. Yet concrete steps to curb CO_2 emissions have only been initiated recently.

In the meantime, CO_2 emissions continue to accelerate: more than 37 billion tonnes of carbon, a new record, were released into the atmosphere in 2018. CO_2 is a natural component of the carbon cycle, involved in such activities as photosynthesis, respiration, volcanic eruptions, and ocean-atmosphere exchange. Human activities, primarily the burning of fossil fuels, deforestation, and changes in land use, release very large amounts of CO_2 to the atmosphere, causing its concentration in the atmosphere to rise, where each molecule may remain for more than 200 years. Cement manufacture, animal agriculture, the clearing of land, and the burning of forests are other human activities that release carbon dioxide.

Scientists look at patterns in data and try to explain differences or deviations from these patterns. As stated in Unit 5.3.1, the atmospheric carbon dioxide data reveal a historical pattern of carbon dioxide increasing and decreasing, cycling between a low of 180 ppm and a high of 300 ppm (Figure 24.2.4). Scientists have concluded that it took around 50,000 years for the atmospheric carbon dioxide level to increase from its low minimum concentration to its higher maximum concentration. However, starting recently, atmospheric carbon dioxide concentrations have increased beyond the historical maximum of 300 ppm. Atmospheric CO_2 concentrations have increased by 45% since pre-industrial times, from approximately 280 parts per million (ppm) in the 18th century to 415 ppm in 2021. What is the reason for this difference in the rate of change and the amount of increase in carbon dioxide? A key factor that must be recognized when comparing the historical data and the current data is the presence of modern human society; no other driver of climate change has yielded changes in atmospheric carbon dioxide levels at this rate or to this magnitude.

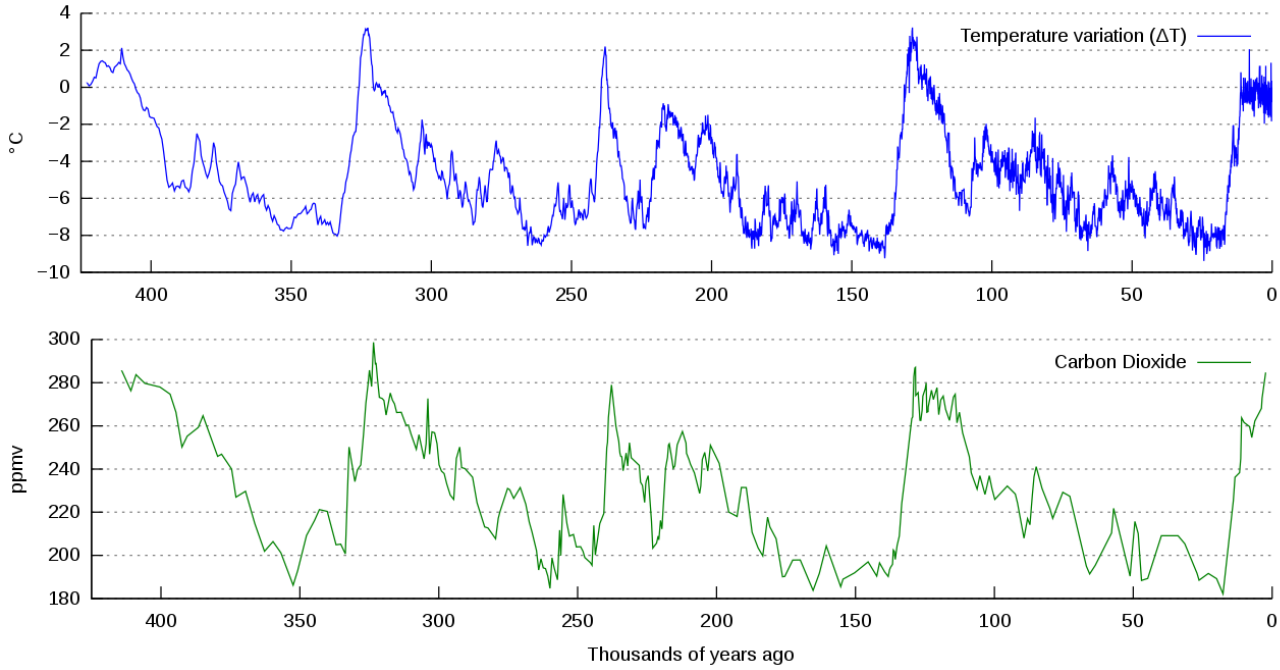


Figure 24.2.4: Graph of change in temperature in degrees Celsius (top, blue line) and carbon dioxide concentration in parts per million by volume (bottom, green line) measured from the Vostok, Antarctica ice core. These have been associated for over 400,000 years. As carbon dioxide concentration increased, so did temperature. As carbon dioxide concentration decreased, so did temperature. These data were collected in 1999. Since then, carbon dioxide concentrations have stabilized to over 410 ppm. Image and caption (modified) by NOAA/Autopilot (CC-BY-SA)

Video



This 4-minute animation describes the natural carbon cycle and how humans are disrupting that cycle. Question after watching: Which of the technologies to remove carbon from the atmosphere have you heard of before? Which have you not? What do these technologies do?

Optional Activity 24.2.2

How long does a molecule of CO_2 remain in the atmosphere?

A. CO_2 washes out of the atmosphere seasonally.
B. CO_2 remains in the atmosphere for 5-10 years.
C. CO_2 remains in the atmosphere for up to 200 years, or more.

Answer

C. CO_2 remains in the atmosphere for up to 200 years, or more.

Optional Activity 24.2.3

What is the primary cause of the overall rising trend in CO_2 in the atmosphere?

A. The increase in CO_2 is caused by burning of fossil fuels.
B. CO_2 is increasing because we are coming out of an ice age.
C. As human population grows, people exhale more CO_2.
D. CO_2 is released by the oceans as they warm.

Answer

A. The increase in CO_2 is caused by burning of fossil fuels.

Methane

Although this concentration is far less than that of CO_2, **methane** (CH_4) is 28 times as potent a greenhouse gas. Methane is produced when bacteria break down organic matter under anaerobic conditions and can be released due to natural or anthropogenic processes. Anaerobic conditions can happen when organic matter is trapped underwater (such as in rice paddies) or in the intestines of herbivores. Anthropogenic causes now account for 60% of total methane release. Examples include agriculture, fossil fuel extraction and transport, mining, landfill use, and burning of forests. Methane can also be released from natural gas fields and the decomposition that occurs in landfills. Specifically, raising cattle releases methane due to fermentation in their rumens producing methane that is expelled from their GI tract. Methane is more abundant in Earth's atmosphere now than at any time in at least the past 650,000 years, and CH_4 concentrations increased sharply during most of the 20th century. They are now more than 2.5 times pre-industrial levels and increasing rapidly.

Another source of methane is the melting of clathrates (methane hydrate). **Clathrates** are frozen chunks of methane hydrate found at the bottom of the ocean. When water warms these chunks of ice melt and methane is released. As the ocean's water temperature increases, the rate at which clathrates melt is increasing, releasing even more methane. This leads to increased levels of methane in the atmosphere, which further accelerates the rate of global warming. This is an example of the positive feedback loop that is leading to the rapid rate of increase in global temperatures. There is strong evidence that warming during the Quaternary period 55 million years ago was caused, at least in part, by a massive release of clathrates.

Video



This 2-minute, 3D volumetric visualization shows the emission and transport of atmospheric methane around the globe between December 9, 2017 and December 1, 2018. (NASA)

Question after watching: What patterns do you notice based on the narrator's descriptions and the visualization?

Other Greenhouse Gases

Nitrous oxide (N_2O) is produced through natural and human activities, mainly through agricultural activities and natural biological processes. Fuel-burning and some other processes also create N_2O. Concentrations of N_2O have risen approximately 18% since the start of the Industrial Revolution, with a relatively rapid increase towards the end of the 20th century. [3] In contrast, the atmospheric concentration of N_2O varied only slightly for a period of 11,500 years before the onset of the industrial period, as shown by ice core samples.

Ground-level ozone (O_3), which also has a short atmospheric lifetime, is a potent greenhouse gas. Chemical reactions create ozone from emissions of nitrogen oxides and volatile organic compounds from automobiles, power plants, and other industrial and commercial sources in the presence of sunlight. In addition to trapping heat, ozone is a pollutant that can cause respiratory health problems and damage crops and ecosystems.

Chlorofluorocarbons (CFCs), hydrochlorofluorocarbons (HCFCs), hydrofluorocarbons (HFCs), perfluorocarbons (PFCs), and sulfur hexafluoride (SF6), together called **F-gases**, are often used in coolants, foaming agents, fire extinguishers, solvents, pesticides, and aerosol propellants. Unlike water vapor and ozone, these F-gases have a long atmospheric lifetime, and some of these emissions will affect the climate for many decades or centuries.

Human-Induced Changes in Albedo and Aerosols

When sunlight energy reaches Earth it can be reflected or absorbed. The amount that is reflected or absorbed depends on Earth's surface and atmosphere. Light-colored objects and surfaces, like snow and clouds, tend to reflect most sunlight, while darker objects and surfaces, like the ocean and forests, tend to absorb more sunlight. The term **albedo** refers to the amount of solar radiation reflected from an object or surface, often expressed as a percentage. Earth as a whole has an albedo of about 30%, meaning that 70% of the sunlight that reaches the planet is absorbed. Sunlight that is absorbed warms Earth's land, water, and atmosphere.

Albedo is also affected by aerosols. **Aerosols** are small particles or liquid droplets in the atmosphere that can absorb or reflect sunlight. Unlike greenhouse gases (GHGs), the climate effects of aerosols vary depending on what they are made of and where they are emitted. Those aerosols that reflect sunlight, such as particles from volcanic eruptions or sulfur emissions from burning coal, have a cooling effect. Those that absorb sunlight, such as black carbon (a part of soot), have a warming effect. In addition, human activities have generally increased the number of aerosol particles in the atmosphere. Overall, human-generated aerosols have a net cooling effect offsetting about one-third of the total warming effect associated with human greenhouse gas emissions. Reductions in overall aerosol emissions can therefore lead to more warming. However, targeted reductions in black carbon emissions can reduce warming.

Human changes in land use and land cover have changed Earth's albedo. Processes such as deforestation, reforestation, desertification, and urbanization often contribute to changes in climate in the places they occur. These effects may be significant regionally but are smaller when averaged over the entire globe.

Video



This 2-minute video visualizes albedo.

Question after watching: What are some human activities that change albedo as visualized in the video?

Climate Feedbacks

When sea ice melts, as it has done in the Arctic Ocean at a disturbing rate over the past decade, the albedo of the area affected changes dramatically, from around 80% down to less than 10%. This is a positive feedback (see a review of feedback loops in Unit 4.4.1) because much more solar energy is absorbed by the water than by the pre-existing ice, and the temperature increase is amplified. The same applies to ice and snow on land, but the difference in albedo is not as great.

When ice and snow on land melt, sea level rises. Sea level is also rising because the oceans are warming and that increases their volume. A higher sea level means a larger proportion of the planet is covered with water, and since water has a lower albedo than land, more heat is absorbed and the temperature goes up a little more. Since the last glaciation, sea-level rise has been about 125m; a huge area that used to be land is now flooded by heat-absorbent seawater. During the current period of anthropogenic climate change, sea level has risen only about 20 cm, and although that does not make a big change to albedo, sea-level rise is accelerating.

Video



A warming Arctic can catapult the world into drastic climate impacts through feedback loops as seen in this 3.5-minute video.

Question after watching: Why should we be concerned with permafrost melting as well as ice in the Arctic?



Figure 24.2.10: A degrading permafrost site on the north coast of Alaska.

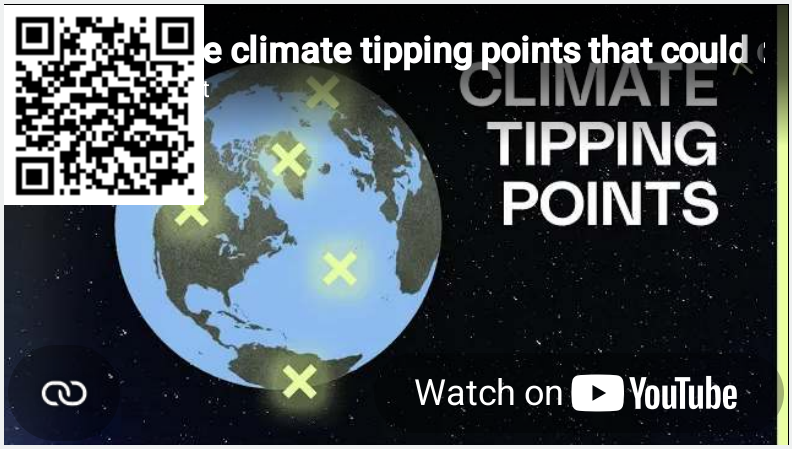
Most of northern Canada has a layer of permafrost that ranges from a few centimeters to hundreds of meters in thickness; the same applies in Alaska, Russia, and Scandinavia. Permafrost is a mixture of soil and ice (Figure 24.2.10), and it also contains a significant amount of trapped organic carbon that is released as CO_2 and CH_4 when the permafrost breaks down. Because the amount of carbon stored in permafrost is in the same order of magnitude as the amount released by burning fossil fuels, this is a feedback mechanism that has the potential to equal or surpass the forcing that has unleashed it. In some polar regions, including northern Canada, permafrost also includes methane hydrate. Breakdown of permafrost releases this form of methane.

There is about 45 times as much carbon in the ocean (as dissolved bicarbonate) as there is in the atmosphere (as CO_2), and there is a steady exchange of carbon between the two reservoirs. But the ability of CO_2 to dissolve in water (its **solubility**) decreases as the temperature goes up. In other words, the warmer it gets, the more oceanic bicarbonate gets released to the atmosphere as CO_2. That makes CO_2 solubility another positive feedback mechanism.

Vegetation growth responds positively to both increased temperatures and elevated CO_2 levels, and so in general, it represents negative feedback to climate change because the more the vegetation grows, the more CO_2 is taken from the atmosphere. However, trees grow bigger and more vigorously so forests have lower albedo so they absorb more heat. In addition, climate change is not just more CO2, it may mean more or less rain, extreme weather events, or drastic seasonal changes that interfere with forest health. Furthermore, climate warming isn't necessarily good for vegetation growth; some areas have become too hot, too dry, or even too wet to support the plant community that was growing there, and it might take centuries for something to replace it successfully.

All of these positive (and negative) feedbacks work both ways. For example, during climate cooling, growth of glaciers leads to higher albedos, and formation of permafrost results in storage of carbon that would otherwise have returned quickly to the atmosphere.

Video



This 3.5-minute video describes climate tipping points.
Question after watching: What is meant by a "tipping point" for climate? What types of systemic changes are studied in terms of climate tipping points? Are these positive feedbacks or negative feedbacks?

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Current and Future Climate Change Impacts

- Please read and watch the following Learning Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 1 hour.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Identify current global climate impacts and their confidence level
- Explain several projected abiotic climate impacts and their effects on living organisms

Introduction

Climate change has the potential to render Earth unrecognizable from what any human has ever experienced. These changes will have an immense impact on ecosystem services, global economies, and our own quality of life. Yet, while there is much talk about these risks, there is still too little action addressing its main causes.

Current Climate Change Impacts

Some of the lack of action may be attributed to “climate change” and “future” often being used in the same sentence, giving politicians and industries a false impression that we can deal with climate change once we achieved sufficient economic growth. The reality could however not be further from the truth, as we already see signs of the changes to come here today (Table 24.3.1), including near-annual crop failures, record-high temperatures, and record-strength coastal storms.

Table 24.3.1: Some examples illustrating how climate change is already impacting our planet (IPCC, 2022).

Impact	Evidence
Increased extreme weather	The rise in weather and climate extremes has led to some irreversible impacts as natural and human systems are pushed beyond their ability to adapt. (high confidence). Widespread, pervasive impacts to ecosystems, people, settlements, and infrastructure have resulted from observed increases in the frequency and intensity of climate and weather extremes, including hot extremes on land and in the ocean, heavy precipitation events, drought, and fire weather (high confidence).
Widespread flood and droughts	Flood and drought-related acute food insecurity and malnutrition have increased in Africa (high confidence) and Central and South America (high confidence).
Rising sea levels	Continued and accelerating sea level rise will encroach on coastal settlements and infrastructure (high confidence) and commit low-lying coastal ecosystems to submergence and loss (medium confidence).
Earlier spring activity	Widespread deterioration of ecosystem structure and function, resilience, and natural adaptive capacity, as well as shifts in seasonal timing have occurred due to climate change (high confidence), with adverse socioeconomic consequences (high confidence).
Disease spread	The occurrence of climate-related food-borne and water-borne diseases has increased (very high confidence). The incidence of vector-borne diseases has increased from range expansion and/or increased reproduction of disease vectors (high confidence). Animal and human diseases, including zoonoses, are emerging in new areas (high confidence).
Shifts in species ranges	Approximately half of the species assessed globally have shifted polewards and to higher elevations on land (very high confidence).
Wildlife population declines	Climate change has caused substantial damages, and increasingly irreversible losses, in terrestrial, freshwater and coastal and open ocean marine ecosystems (high confidence). The extent and magnitude of climate change impacts are larger than estimated in previous assessments (high confidence). Hundreds of local losses of species have been driven by increases in the magnitude of heat extremes (high confidence), as well as mass mortality events on land and in the ocean (very high confidence) and loss of kelp forests (high confidence). Some losses are already irreversible, such as the first species extinctions driven by climate change (medium confidence).

Terms from Table 24.3.1

Risk: provides a framework for understanding the increasingly severe, interconnected, and often irreversible impacts of climate change on ecosystems, biodiversity, and human systems; differing impacts across regions, sectors, and communities; and how to best reduce adverse consequences for current and future generations.

Adaptation: in human systems, the process of adjustment to actual or expected climate and its effects in order to moderate harm or take advantage of beneficial opportunities. In natural systems, adaptation is the process of adjustment to actual climate

and its effects; human intervention may facilitate this.

Resilience: the capacity of social, economic, and ecosystems to cope with a hazardous event, trend, or disturbance, responding, or reorganizing in ways that maintain their essential function, identity, and structure as well as biodiversity in case of ecosystems while also maintaining the capacity for adaptation, learning, and transformation.

Mitigation: reducing emissions, and stabilizing the levels, of heat-trapping greenhouse gases in the atmosphere.

Confidence: each finding is grounded in an evaluation of underlying evidence and agreement. A level of confidence is expressed using five qualifiers: very low, low, medium, high and very high.

Between June 25 and July 1, 2021, British Columbia experienced a massive heat dome with temperatures reaching 49.6^{o}C in some areas. Scientists have stated that climate change was a contributing factor. More than 500 deaths were attributed to the heat. Glaciers throughout British Columbia are in retreat, with losses ranging from 6% to 34% from 1985-2005, and their melting is increasing. See more from the British Columbia Provincial Government: Change in Size of B.C. Glaciers.

A summary of the impacts of climate change on natural disasters is given in Figure 24.3.1. The major types of disasters related to climate are floods and storms, but the health implications of extreme temperatures are also becoming a great concern. In the decade 1971 to 1980, extreme temperatures were the fifth most common natural disasters; by 2001 to 2010, they were the third most common.

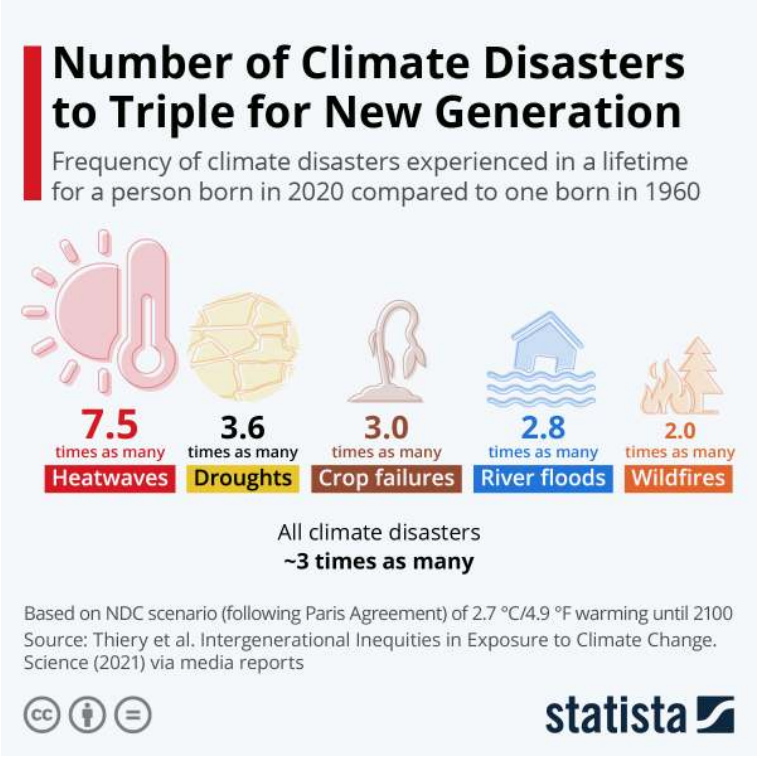
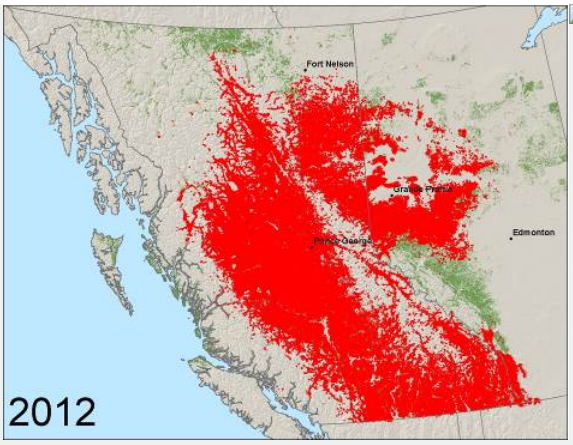


Figure 24.3.1: Predicted future climate disasters for someone born in 2020 versus someone born in 1960.

Canadian Perspective - The Mountain Pine Beetle

"The mountain pine beetle (*Dendroctonus ponderosae* Hopkins) is native to western North America, from northern Mexico to northern British Columbia. It is also present in an isolated population of pine that is surrounded by prairie in the Cypress Hills area of southwestern Saskatchewan, which was likely infested in the early 1980s. In the 2000s, the beetle significantly expanded its range in Canada, invading new habitat east of the Rocky Mountains in northeastern British Columbia and northern Alberta (Figure 24.3.2 left)."[1]



Reddened pine, caused by pine beetle attack, in central British Columbia.

Figure 24.3.2: Left: Observed presence of mountain pine beetle from 1999 to 2012 (Government of Canada). Right: Large area of damaged forest (Government of British Columbia)

"Most species of pine that grow in the beetle's range are readily attacked, with the exception of Jeffrey pine. In Canada, these hosts include ponderosa, western white, whitebark, limber pines, and, very recently, jack pine in the expanded range. Lodgepole pine is the most common host in the mountain pine beetle's range in British Columbia."[1]

"This small beetle attacks and kills mature trees by boring through the bark and mining the phloem (living tissue in vascular plants that carries organic nutrients). Its eggs hatch into larvae that consume the phloem, killing the tree. The beetles are killed by very cold winter weather, which historically has kept their numbers in check."[2]

"Trees will attempt to repel the beetles by releasing quantities of resin, which mixes with the boring dust and forms a soft, white or reddish pitch tube around each borehole. These pitch tubes usually appear from the duff line to a top diameter of 15cm. Infected trees' foliage turns yellow and then red by the spring of the year following the initial beetle attack. Most of the needles drop from the tree after two years, leaving a dead grey snag."[2]

"In British Columbia, the northern limit of the beetle's range has been limited by cold winter temperatures (−40°C) and cool summers. Outbreaks have been linked to favorable weather in both summer and winter. Warm, dry summers are good for beetle development and dispersal, and drought stress reduces tree defenses. In the late 1990s, after several relatively warm winters, a massive outbreak resulted in the loss of millions of hectares of pine forest in British Columbia over the next 15 years."[1,2]

Resources:

1. Government of Canada. 2021. *Mountain pine beetle (factsheet)*. Natural Resources Canada [Online]. Available from: https://www.nrcan.gc.ca/forests/fire-insects-disturbances/top-insects/13397

2. Government of British Columbia. 2022. *Mountain pine beetle.* Forest Health [Online]. Available from: https://www2.gov.bc.ca/gov/content/industry/forestry/managing-our-forest-resources/forest-health/forest-pests/bark-beetles/mountain-pine-beetle

Future Climate Change

Many greenhouse gases stay in the atmosphere for long periods of time. As a result, even if emissions stopped increasing, atmospheric greenhouse gas concentrations would continue to remain elevated for hundreds of years. Moreover, if we stabilized concentrations and the composition of today's atmosphere remained steady (which would require a dramatic reduction in current greenhouse gas emissions), surface air temperatures would continue to warm (Figure 24.3.3). This is because the oceans, which store heat, take many decades to fully respond to higher greenhouse gas concentrations. The ocean's response to higher greenhouse gas concentrations and higher temperatures will continue to impact climate over the next several decades to hundreds of years. Thus, past and present GHG emissions will affect climate far into the future.

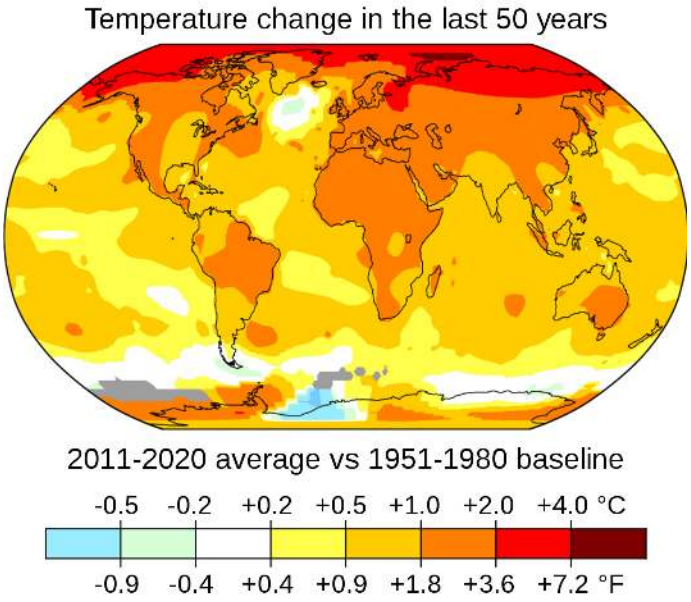


Figure 24.3.3: Temperature increases have been most pronounced in northern latitudes and over land masses. The colors represent the temperature difference between the 2011-2020 average and the 1951-1980 baseline, with warmer colors (yellow, orange, red) representing increases, and cool colors (green, blue) representing decreases. The image uses longer term averages of at least a decade to smooth out climate variability due to factors such as El Niño. Grey areas in the image have insufficient data for rendering. Image and caption (modified) from NASA's Scientific Visualization Studio/Eric Fisk (public domain).

Temperature Changes

Climate models project the following key temperature-related changes:

- Average global temperatures are expected to increase by 1.1°C to 6.4°C by 2100, depending on the level of future greenhouse gas emissions, and the outcomes from various climate models.
- By 2100, global average temperature is expected to warm at least twice as much as it has during the last 100 years.
- Ground-level air temperatures are expected to continue to warm more rapidly over land than oceans.
- Some parts of the world are projected to see larger temperature increases than the global average.

These changes will impact our food supply, water resources, infrastructure, ecosystems, and even our own health. The magnitude and rate of future climate change will primarily depend on the following factors:

- The rate at which levels of greenhouse gas concentrations in our atmosphere continue to increase, often known as "climate scenarios" (Figure 24.3.4);
- How strongly features of the climate (e.g., temperature, precipitation, and sea level) respond to the expected increase in greenhouse gas concentrations; and
- Natural influences on climate (e.g., from volcanic activity and changes in the sun's intensity) and natural processes within the climate system (e.g., changes in ocean circulation patterns).

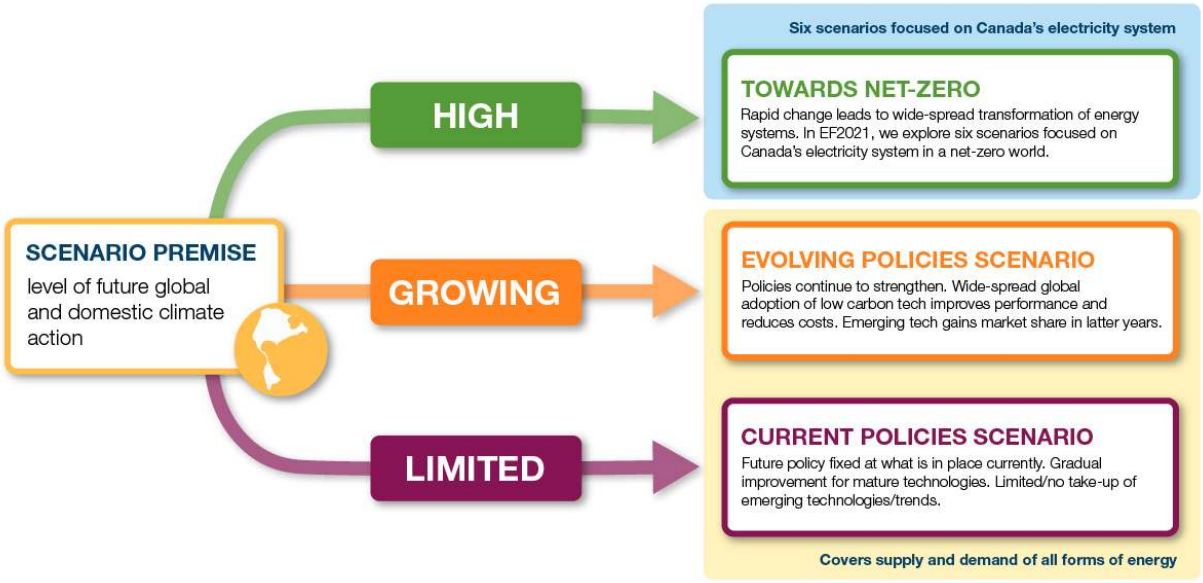


Figure 24.3.4: Conceptual illustration of Canada's energy and climate scenarios, 2021. The first main scenario is the Evolving Policies Scenario. The premise of this scenario is that there is *growing* action to reduce the GHG emissions from our energy system at a pace similar to recent history, in both Canada and the world. Relative to a scenario with less action to reduce GHG emissions, this projection implies less global demand for fossil fuels, and greater use of low-carbon technologies. The second main scenario is the Current Policies Scenario, which assumes *limited* action to reduce GHGs beyond policies already in place today. The third main set of scenarios explores a net-zero future with a *high* level of global and domestic climate action. Specifically, the set of scenarios in the Net-Zero premise explore what Canada's electricity grid might look like in a net-zero world under six different sets of assumptions about future technologies, climate policies, and electricity use. (Government of Canada - Canada Energy Regulator)

Species that are highly mobile are not entirely spared from the negative impacts of climate change. Consider that migratory species rely on environmental cues, such as day length and temperature, to determine when to start moving from one area to the next. But because different species rely on different environmental cues to time their life cycles (e.g. breeding), not all species will adjust to climate change at the same rate. There is consequently a high likelihood that climate change will disrupt these synchronous movements that the animals in particular have developed over thousands to millions of years. This disruption of timed aspects of a species' life cycle, such as migration and breeding, is called **phenological mismatch**. Researchers have already seen signs of phenological mismatch: some migratory birds that overwinter in the tropics have started to migrate to their breeding grounds at earlier dates than before. If these trends hold, they may soon start breeding before peak food availability, which could lead to lower fitness of offspring.

Resident species are also vulnerable to phenological mismatch. While these species might not be known for large-scale movements around the globe, they may still have to adjust their ranges to keep track of their climatic niches. Considering the improbability that different species will all adapt at the same pace, there is thus a danger that important mutualistic relationships might be pulled apart during these range adaptations. This is of concern for species with specialized feeding niches, as seen in some pollinators. Extinctions arising from this decoupling of mutualistic relationships are referred to as **coextinction**.

Freshwater ecosystems will generally experience temperature increases under climate change. Like their terrestrial counterparts, many freshwater species are sensitive to temperature shifts as warmer water also holds less dissolved oxygen. In addition, longer growing seasons and higher water temperatures will lead to increased nutrient loads, algae blooms, and eutrophication. All these factors will force many freshwater species—even those not sensitive to temperature shifts—to adjust their ranges to keep track of suitable conditions. For some freshwater species, the impediments to adjusting their ranges as necessary may be insurmountable.

Not all species will be impacted negatively. A variety of species are expected to benefit from climate change. These include generalist species currently limited by interactions with localized specialists that are—at least at present—better competitors for limiting resources. Some tropical species may thrive as their habitats become hotter and wetter. Species with high genetic diversity that reproduce quickly (allowing for rapid adaption to environmental changes) are also likely to benefit. Unfortunately, many species that exhibit these traits carry diseases and/or are agricultural pests. For example, populations of the coffee berry borer (*Hypothenemus hampei*)—Africa's most notorious coffee pest—are expected to greatly increase in a warmer world. This growing

threat is particularly worrying given that higher temperatures have already reduced coffee harvests in countries such as Tanzania by as much as 50%.

The range of disease-carrying insects and the viruses and pathogenic parasites they harbor will increase. This spread has already been documented in North America with several different diseases including West Nile and Lyme disease. Colder temperatures typically limit the distribution of certain species, such as the mosquitoes that transmit malaria, because freezing temperatures destroy their eggs. Not only will the range of some disease-causing insects expand, but increasing temperatures will also accelerate the host lifecycles, allowing them to breed and multiply more quickly. They may even evolve pesticide resistance faster. In addition to those listed above, other diseases such as dengue fever, malaria, yellow fever, zika virus, and chikungunya are expected to spread to new regions as the global climate warms.

Climate change does not only increase the spread of diseases in humans. Rising temperatures are associated with greater amphibian mortality due to chytridiomycosis (see Unit 5.2.3). Similarly, warmer temperatures have exacerbated bark beetle infestations of coniferous trees, such as pine and spruce.

? Optional Activity 24.3.1

How do climate factors (temperature, precipitation, & humidity) relate to vector-borne disease?

A. Heavy rain increases the risk of animals transmitting pathogens.
B. Milder winters increase the vector density & risk of disease
C. Dry summers & drought increase the risk of vectors expanding their range
D. More intense snowstorms Snow increase vector density & risk of disease

Answer

B. Milder winters increase the vector density & risk of disease.

Precipitation and Storm Events

Patterns of precipitation and storm events, including both rain and snowfall are likely to change. However, some of these changes are less certain than the changes associated with temperature. Because warm air is able to hold more water than cold air, the general global trend over the past century has been one of increasing precipitation (Figure 24.3.5).

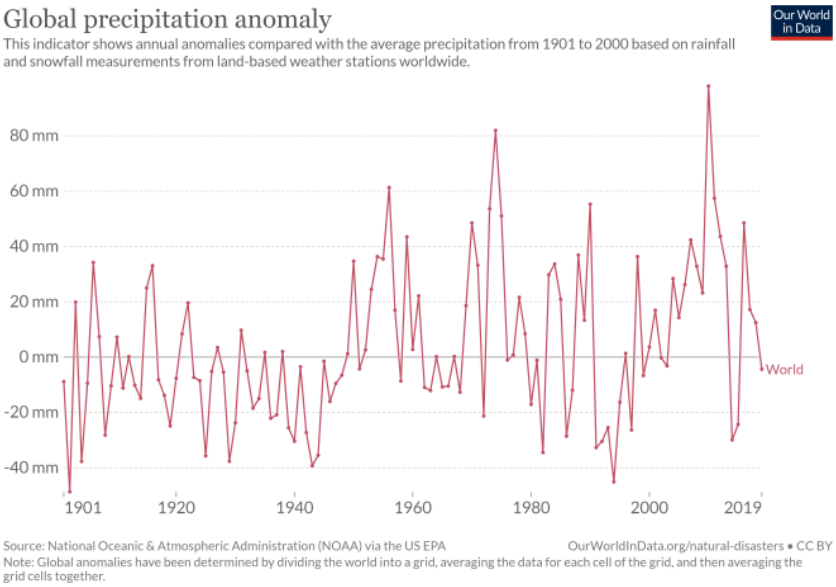


Figure 24.3.5: Data shows global precipitation patterns, based on rainfall and snowfall measurements from land-based weather stations worldwide. This indicator shows annual anomalies, or differences, compared with the average precipitation from 1901 to 2000. CC-BY United States Environmental Protection Agency (EPA)

Projections show that future precipitation and storm changes will vary by season and region. Some regions may have less precipitation, some may have more precipitation, and some may have little or no change. The amount of rain falling in heavy precipitation events is likely to increase in most regions, while storm tracks are projected to shift toward the poles. Climate models project the following precipitation and storm changes:

- Global average annual precipitation through the end of the century is expected to increase, although changes in the amount and intensity of precipitation will vary by region.
- The intensity of precipitation events will likely increase on average. This will be particularly pronounced in tropical and high-latitude regions, which are also expected to experience overall increases in precipitation.
- The strength of the winds associated with tropical storms is likely to increase. The amount of precipitation falling in tropical storms is also likely to increase.
- Annual average precipitation is projected to increase in some areas and decrease in others.

One of the other risks for coastal populations, besides sea-level rise, is that climate warming is also associated with an increase in the intensity of coastal storms (e.g., atmospheric rivers, hurricanes, cyclones, or typhoons), which almost always bring serious flooding from intense rain and storm surges. Some recent examples are the Vancouver floods of 2021 and the impact of Hurricane Fiona on Nova Scotia in 2022 (Figure 24.3.6).

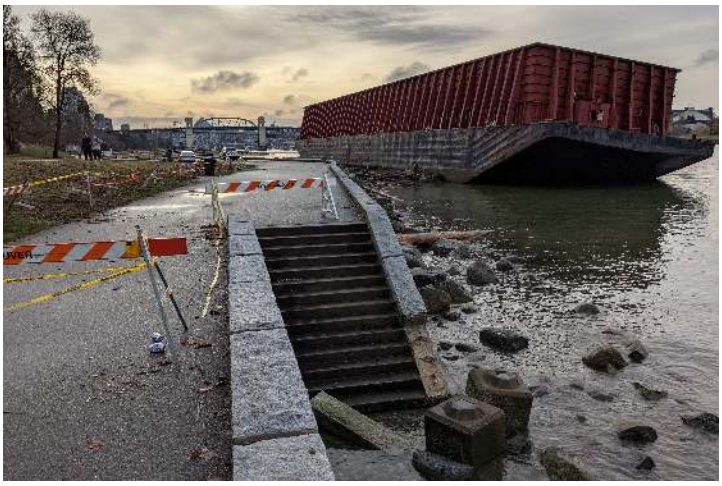


Figure 24.3.6: Grounded barge along Vancouver's Seawall in English Bay. November 2021. CC-BY-SA 4.0 Northwest

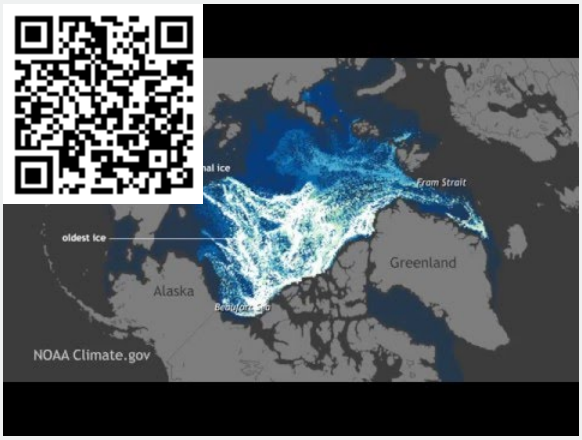
Changing precipitation levels will have several impacts on freshwater ecosystems, particularly as it relates to changes in their flow regimes. For example, areas that are undergoing decreased precipitation will experience decreased runoff and increased drying of wetlands and small streams, while areas with increased precipitation will experience increased storm surges and flushing. Given these multiple stressors, there is a reasonable expectation that many freshwater species will go extinct or face significant population declines and range shifts over the next decades. These changes are of major concern in countries that are currently majority subsistence, where so many people depend on fish and related natural resources for their livelihoods. Many communities around the world are already finding it more difficult to meet their nutritional needs due to climate-induced freshwater fish declines. Also, at some large lakes, which may supply 20–40% of the surrounding countries' dietary protein—fish yields have decreased by 30% in recent years, also attributed to climate change.

Ice Melt and Sea Level Rise

Arctic sea ice is already declining. Sea ice is ice floating in the ocean (not on land like a glacier). Most sea ice is in the Arctic Ocean and the extent of sea ice is shrinking. Below, the NOAA animation shows how perennial sea ice has declined from 1990 to 2015. The oldest ice is white and the youngest (seasonal) ice is dark blue. The amount of old ice has declined from 20% in 1985 to 3% in 2015. For every 1°C of warming, models project about a 15% decrease in the extent of annually averaged sea ice (the total ice extent and concentration averaged over a year) and a 25% decrease in September Arctic sea ice.

Video





This 2-minute video from the US's National Oceanic and Atmospheric Association illustrates the loss of Arctic sea ice from 1990-2015.

Question after watching: What seasonal patterns do you notice? What do you notice regarding the oldest ice over the 25 years portrayed in the video?

The land-based, coastal sections of the Greenland and Antarctic ice sheets have been melting significantly and are expected to continue to do so (Figure 24.3.7). If the rate of this ice melting increases in the 21st century, these ice sheets could add significantly to global sea level rise and disrupt global ocean currents. Before anthropogenic warming, glacial activity was variable with some retreating and some advancing. Now, nearly all glaciers globally a retreating and expected to continue to melt, leading to freshwater shortages globally.

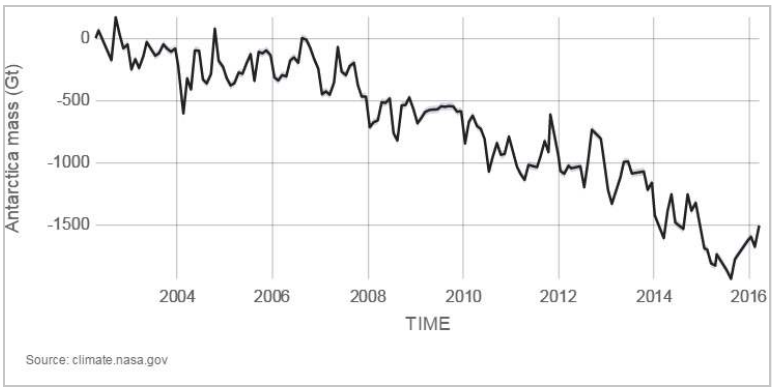


Figure 24.3.7: Decline of Antarctic ice mass from 2002 to 2016. (NASA)

On average, the sea is rising at a rate of 1.8 mm per year. However, between 1993 and 2010 the rate of sea level increase ranged between 2.9 and 3.4 mm per year (Figure 24.3.8). This is thought largely to be from both the melting of glaciers and thermal expansion. Thermal expansion means that as objects such as solids, liquids, and gases heat up, they expand in volume. Since 1970, the melting of glaciers and thermal expansion account for 75% of the sea-level rise (scientists are still researching the other 25%). As the oceans creep further inland, the extent of low-lying coastal ecosystems such as rocky shores or sandy beaches will shrink, and so also the sizes of the wildlife populations living in those areas.

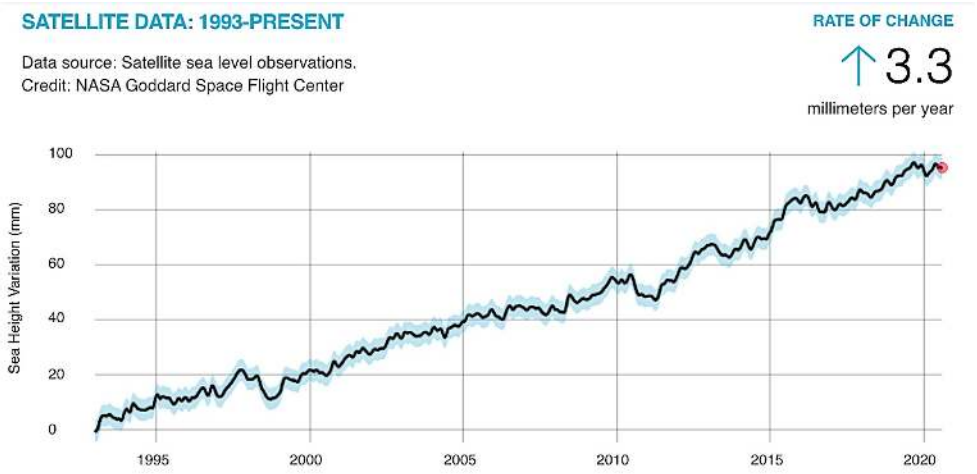


Figure 24.3.8: Sea height variation (mm) over time. Sea height has increased about 3.3 millimeters per year on average since 1993. Data is from satellite sea level observations by the NASA Goddard Space Flight Center. Image by NASA (public domain)

Projections for sea level rise to the end of this century vary widely. This is in large part because we do not know which of the above climate change scenarios (Figure 24.3.3) we will most closely follow, but many are in the range from 0.5 m to 2.0 m. One of the problems in predicting sea level rise is that we do not have a strong understanding of how large ice sheets, such as Greenland and Antarctica, will respond to future warming. Another issue is that the oceans do not respond immediately to warming. For example, with the current amount of warming, we are already committed to a future sea level rise of between 1.3 m and 1.9 m, even if we could stop climate change today.

? Optional Activity 24.3.2

What are the major causes of sea level rise?

A. Melting sea ice
B. Melting glaciers and ice sheets
C. Seawater expanding as it gets warmer
D. A and B
E. B and C

Answer

B and C. Melting glaciers and ice sheets and seawater expanding as it gets warmer.

Ocean Acidification and Deoxygenation

Since 1750, the ocean has absorbed about 30% of all anthropogenic carbon dioxide sources. When carbon dioxide gets absorbed in the ocean, it creates carbonic acid which makes the ocean more acidic. **Ocean acidification** is the process of ocean waters' decreasing pH (lower values are more acidic on the pH scale). The pH level of the oceans has decreased by approximately 0.1 pH units since pre-industrial times, which is equivalent to a 25% increase in acidity. The pH level of the oceans is projected to decrease even more by the end of the century as CO_2 concentrations are expected to increase for the foreseeable future.

Ocean acidification adversely affects many marine species, including plankton, mollusks, shellfish, and corals. As ocean acidification increases, the availability of calcium carbonate will decline. Calcium carbonate is a key building block for the shells and skeletons of many marine organisms. Most tropical oceans have experienced extensive coral bleaching events in recent years due to increased sea surface temperatures and ocean acidification. Ocean acidification also disturbs predator-prey dynamics by impairing the senses of prey species and compromising the ability of marine creatures to communicate with those within their same species.

Marine fish and invertebrates rely on dissolved oxygen that enters the water either through the atmosphere or by photosynthetic plankton. But because warmer water absorbs less oxygen, scientists predict that some areas of the ocean will see a 3–6% drop in dissolved oxygen concentrations under climate change. This process, known as **ocean deoxygenation**, will leave parts of the ocean unsuitable for marine fishes and invertebrates, leading to dead zones. The impact of ocean deoxygenation will also be felt by economically important fisheries where climate change is predicted to lead to fisheries-related economic losses upwards of $415 million each year.

Acidification combined with warmer temperatures and lower oxygen levels is expected to have severe impacts on marine ecosystems, especially coral reefs, and associated fisheries possibly affecting our ocean-derived food sources.

? Optional Activity 24.3.3

What causes ocean acidification?

A. Deoxygenated ocean water.
B. Ocean pollution.
C. Warm freshwater from land.
D. CO_2 dissolved in ocean water.

Answer

D. CO_2 dissolved in ocean water.

Climate Change Affects Everyone

We have all experienced the effects of climate change over the past decade. However, it is not straightforward for climatologists to make the connection between a warming climate and specific weather events, and most are justifiably reluctant to ascribe any specific event to climate change. In this respect, the best measures of climate change are those that we can detect over several decades, such as the temperature changes shown in Figure 24.3.2, or the sea level rise shown in Figure 24.3.7.

Our lives are connected to the climate**.** Human societies have adapted to the relatively stable climate we have enjoyed since the last ice age which ended several thousand years ago. A warming climate will bring changes that can affect our water supplies, agriculture, power and transportation systems, the natural environment, and even our own health and safety. Carbon dioxide can stay in the atmosphere for nearly a century, on average, so Earth will continue to warm in the coming decades. The warmer it gets, the greater the risk for more severe changes to the climate and Earth's system. Although it is difficult to predict the exact impacts of climate change, what is clear is that the climate we are accustomed to is no longer a reliable guide for what to expect in the future.

Indigenous Connections: Climate Change Vulnerabilities

In 2019, the Tsleil-Waututh Nation published a report entitled, "Understanding Our Community's Climate Change Vulnerabilities: Community Climate Change Resilience Planning | PHASE 1 Summary". As noted in the report, "Climate change has the potential to profoundly impact the Tsleil-Waututh Nation (TWN) and many key aspects of community life. It influences the ability of our community to harvest some wild foods and medicinal plants, how we access the shoreline and marine waters, and how we connect with Nature. It poses community health risks, influence our ability to practice spiritual and cultural ceremonies, and share cultural teachings...This report serves to build an understanding of community vulnerability to climate change and begins to explore potential climate adaptation actions" (Tsleil-Waututh Nation, 2019).

The project focused on "climate change impacts to Tsleil-Waututh, also known as Burrard Inlet IR#3, which is the current village site for the Nation. In the future, TWN hopes to expand the assessment to consider the vulnerability of other areas within its traditional territory" (Tsleil-Waututh Nation, 2019).

Below is a summary of some of what this report details as possible impacts of climate change on the Tsleil-Waututh Nation:

- Coastal flood hazard modeling results showed that most waterfront properties may experience flooding during an extreme flood under a 2 m sea level rise scenario.
- Coastal erosion may affect waterfront properties and natural habitats, and threaten buildings, archeological, and other cultural sites.
- Ocean acidification from climate change poses an acute threat to species (particularly shellfish) along the mudflats and beaches of Burrard Inlet IR#3.
- [Loss of intertidal areas] will have significant impacts on species that live in the intertidal zone (e.g., shellfish) or that forage for food in these areas (e.g., marine birds and salmon). Many of these species are critically important as sources of food for TWN community and cultural health and serve as important opportunities to share traditional teachings (Figure 24.3.9).
- The waters of Burrard Inlet will be increasingly vulnerable to harmful algal blooms as water temperatures rise and summer precipitation decreases.
- Climate change has the potential to make local waters more habitable for invasive non-native species, particularly those from warmer waters.
- Extended periods of extreme heat can cause heat exhaustion or heat stroke, particularly among vulnerable groups.
- Community member health and the opportunity for recreation, cultural practices, and job productivity is also impacted by poor air quality and smoke from wildfires across BC.
- Ongoing changes to air temperatures and precipitation patterns from climate change could increase the success and abundance of some invasive species.



Figure 24.3.9: A keystone species, the ochre sea star (*Pisaster ochraceus*) taken at Ganges Harbour, Salt Spring Island, British Columbia, CC-BY-SA D. Gordon E. Robertson

Reference:

Tsleil-Waututh Nation. 2019. "Understanding Our Community's Climate Change Vulnerabilities: Community Climate Change Resilience Planning | PHASE 1 Summary" British Columbia, Canada. Available from: https://twnation.ca/wp-content/uploa...e-Jan-2020.pdf

Video



Learn how climate change will transform British Columbia by 2050 in this 3.5-minute video by CBC's Johanna Wagstaffe.

Question after watching: Which of the changes will affect you directly? Which of the changes will affect you indirectly?

Suggested Supplementary Reading

Intergovernmental Panel on Climate Change. 2021. 6th Assessment: Summary for Policymakers.

NASA. 2022. Global Climate Change: Vital Signs of the Planet. This website by NASA provides a multi-media smorgasbord of engaging content. Learn about climate change using data collected by NASA satellites and more.

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24.4: Climate Strategies

Climate Strategies

- Please read and watch the following Learning Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 1 hour.
- Optional Activities are embedded.

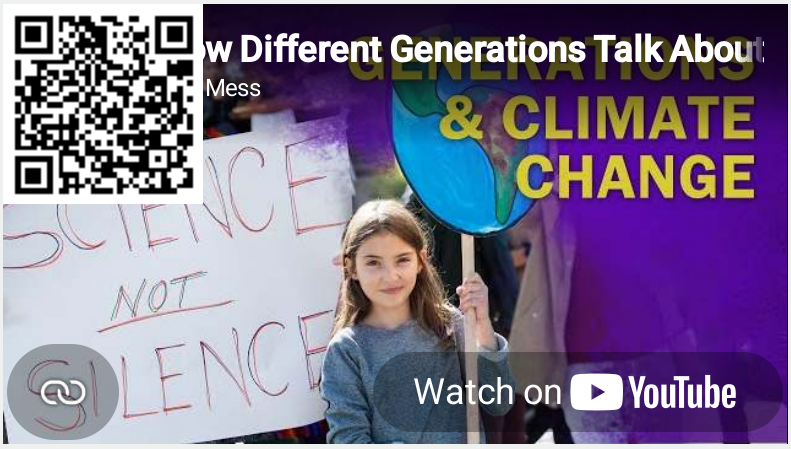
Learning Objectives

- Explain the global efforts to communicate about, and combat, climate change
- Describe the differences between adaptation and mitigation strategies

Introduction

With the increase in understanding that our activities are creating a global crisis of epic proportions, the impacts of climate change are now being actively debated in the corridors of governments and major corporations. Politicians, the media, and others are also increasingly replacing “climate change” with more vivid language, like “climate crisis” and “climate emergency.” This will hopefully encourage even more governments and industries to come to the table and cooperate like never before to address the fundamental drivers of climate change. Solving this global crisis requires an international multi-pronged approach that should include ecosystem protection, restoration, direct species management, reduction of carbon emissions, sustainable planning, and legislative action.

Video



What’s changed since the early days of the environmental movement? How are the stakes different today? And what’s the best way to speak up about climate change?

International Agreements

On the international front, key initiatives related to research and planning are being led by the United Nations Environment Programme (UNEP) and the World Meteorological Organization (WMO), which in 1988 established the Intergovernmental Panel on Climate Change (IPCC). The IPCC undertakes comprehensive reviews of the science of global warming, with a focus on likely scenarios of climatic, ecological, and economic consequences. The IPCC also does research on ways to slow or prevent the increases in GHGs and on how economic and ecological systems might adapt to predicted climate change. At the international level, the IPCC is the most credible source of information about climate change.

Because of concerns about the potentially disastrous consequences of global warming, in 1990 the IPCC and other groups of climate specialists recommended that the United Nations (UN) mobilize global leadership to negotiate an international agreement to reduce emissions of GHGs. The UN then established an Intergovernmental Negotiating Committee to draft the terms of a **UN**

Framework Convention on Climate Change (UNFCCC). After a series of difficult international negotiations, the UNFCCC was drafted and then adopted in 1992 at the UN Conference on Environment and Development (UNCED) held in Rio de Janeiro, Brazil.

The objective of the UNFCCC is to stabilize atmospheric GHGs at concentrations that would prevent a dangerous intensification of the planetary greenhouse effect. Signatory nations to the UNFCCC, known as “parties to the convention,” have agreed to undertake certain actions to compile information on emissions of GHGs, develop policies to decrease emissions, prepare strategies to adapt to anticipated effects of climate change, and provide financial and scientific support to developing countries. Moreover, the 140 countries that signed the UNFCCC in Rio agreed to discuss its implementation at a global forum, which was held in Berlin in 1995. At that meeting, it was agreed that global emissions of GHGs should be reduced and a further series of international negotiations was needed to reach consensus on an implementation strategy. Those negotiations were completed at another meeting, held in Kyoto, Japan, in 1997. The outcome of that key meeting was the **Kyoto Protocol**.

Most years, since 1992, the world's countries have come together to renegotiate and discuss climate change at an UN-organized **Conference of the Parties** (Parties meaning those who signed to the UNFCCC), also known as "COP". As of 2022, COP27 was held in Egypt celebrating the 30th Anniversary of the ratification of the UNFCCC where attendees from 197 countries met to discuss solutions, financing, and collaboration.



Figure 24.4.1: Young people demand action to protect their futures at the 2021 UN Climate Change Conference, also known as COP26, held in Glasgow, Scotland. Photograph by UNFCCC, https://ukcop26.org/young-people-dem...ures-at-cop26/, Open Government Licence(OGL).

National and Local Action

The US never ratified the Kyoto Protocol, and, like most other developed countries, the US has not produced an effective strategy for meeting its legal obligations under agreements that followed, largely because of the intense political and economic controversies associated with the actions that would be necessary. Moreover, the government to date has focused on individual action and intensity-based targets, which encourage improved technological efficiencies but do not necessarily reduce the aggregate emissions of GHGs. Such tactics do little to reduce the rapid increase of emissions from increased industry and new fossil fuels coming online like the rapid expansion of natural gas in the last 30 years.

Climate policies have ebbed and flowed under the five presidential administrations since the Kyoto Protocol. During the Trump Administration (2017-2021), information regarding climate change and policies was removed from the internet. Under the Biden Administration, climate policies and agreements were reinstated and new short- and long-term strategies have been put forward. A primary goal is to reduce carbon emissions to 50-52% of 2005 levels by 2030. To achieve this, the following targets have been identified:

- Electricity: 100% carbon pollution-free electricity system by 2035 (backbone of the current climate policy)
- Transportation: 50% of all new light-duty cars to be zero emission by 2030; infrastructure to support all clean transportation (rail/tram, bike, pedestrian, etc.)
- Buildings: Improve energy efficiency and increase the sales share of clean and efficient electric appliances
- Industry: Focus on industrial decarbonization (energy efficiency, low-carbon fuels, industrial carbon capture and sequestration [see below])
- Agriculture, Forestry, and Land Use: Reduce agricultural methane and N_2O emissions; enhance forest protection and management; promote natural carbon sequestration forests and soils

Video



Popular support for climate action hasn't been translated into actual bold steps to reduce America's reliance on fossil fuels. So why is there this big discrepancy?

In addition, to combat climate change, the leadership of many states, counties, and cities have enacted laws and policies to reduce greenhouse gas emissions and habitat destruction in their own communities. Some industries are hard at work developing "greener" technologies to enable us to live more sustainably. Communities are coming together to implement solutions that are a best-fit for local environments and economies. Conservation biologists also play a crucial role in mitigating the negative impacts of climate change. In addition to highlighting the plight of the natural world to society at large, we could work towards reducing the loss of ecosystem services and preventing species extinctions. To accomplish this task, we need to identify which species and ecosystems are most sensitive to climate change and develop strategies that will ensure the continued persistence of as many sensitive species and their habitats as possible.

Video



Why is your local government so much better set up for implementing climate solutions than the federal government?

The situation surrounding global climate change is in serious need of our attention. It is important to realize that many scientists, leaders, and concerned citizens are making solutions to climate change part of their life's work (Figure 24.4.1). The two solutions to the problems caused by climate change are mitigation and adaptation, and we will likely need a combination of both in order to prosper in the future.

Video



The UN's Sustainable Development Goals (SDGs) outline issues and strategies for the future of humans and natural systems. This 8.5-minute video describes SDG 13, which is focused on Climate Action.
Question after watching: Which of the strategies have you heard of before? Which strategies are new to you? What barriers to change resonate with you? What actions can you take to make change happen?

Climate Mitigation Strategies

In general, a strategy to mitigate climate change is one that reduces the amounts of greenhouse gases in the atmosphere or prevents additional emissions. Mitigation strategies attempt to “fix” the problems caused by climate change.

Greenhouse Gas Reduction

There are many options for reducing the adverse impacts to society from CO_2 and other greenhouse gas emissions, such as switching to sources of electricity that do not contribute to the CO_2 problem, trying to generate fossil-based electricity by not releasing the CO_2 into the atmosphere, or exploring ways to reduce the demand for products that produce greenhouse gas emissions. Governmental regulations regarding the fuel efficiency of vehicles is one example of an institutionalized mitigation strategy already in place in many countries around the world.

Putting a price on carbon is the method many economists favor for reducing or controlling greenhouse gas emissions. Pricing carbon provides producers and consumers with a monetary incentive to reduce greenhouse gas emissions by placing a value on each unit of carbon dioxide or carbon dioxide equivalent that is emitted into the atmosphere. The US currently does not have a carbon tax, even as it has been debated in the House and Senate for many legislative sessions. However, we can look to Canada for a system of **carbon taxes,** or charges for burning fossil fuels, to see how this might work to help society reduce greenhouse gases collectively.

Canada's "carbon pollution pricing system" has been in place since 2019. The federal pricing system has two parts: a regulatory charge on fossil fuels like gasoline and natural gas, known as the **Fuel Charge**, and a performance-based system for industries, known as the **Output-Based Pricing System**. Each province or territory can design its own pricing structure or the region will default to the Canadian government's minimum national stringency standards (known as the Federal Backstop) (Figure 24.4.2). Currently, this pricing mechanism is in place for the burning of fossil fuels such as gasoline or natural gas and for industries.

"Proceeds from the federal carbon pricing system remain in the jurisdiction where they were collected. Provinces and territories that requested the federal system receive these proceeds directly and can use them as they see fit. In other jurisdictions, the federal government delivers all proceeds to individuals, families, and businesses through payments and climate action programs. This helps make carbon pricing affordable, and enables households to make investments to increase energy efficiency and further reduce emissions" (Government of Canada, 2022). This type of governmental mitigation strategy has been shown to be effective in many other countries including India, Japan, France, Costa Rica, Canada, and the United Kingdom.



Figure 24.4.2: The provinces and territories on the map of Canada are one of three colors depending on whether the federal backstop applies in full, in part or not at all. CC-BY-SA Government of Canada

Video



The average carbon footprint of a person in the US is 16.5 tons. So, what can you actually do to decrease this number and make a meaningful difference?

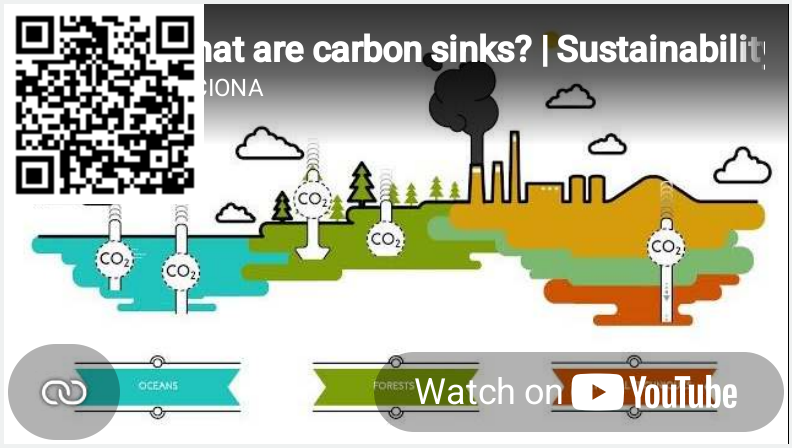
Carbon Capture and Sequestration

In addition to government measures and incentives, technology can also be harnessed to mitigate climate change. One strategy for this is the use of **carbon capture and sequestration** (CCS). Through CCS, 80-90% of the CO_2 that would have been emitted to the atmosphere from sources such as a coal-fired power plant is instead captured and then stored deep beneath the Earth's surface. The CO_2 is often injected and sequestered hundreds of miles underground into porous rock formations sealed below an impermeable layer, where it is stored permanently.

Scientists are also looking into the use of soils and vegetation for carbon storage potential. Proper management of soil and forest ecosystems has been shown to create additional carbon sinks for atmospheric carbon, reducing the overall atmospheric CO_2 burden. Increasing soil carbon further benefits communities by providing better-quality soil for agriculture and cultivation.

Technologies related to alternative energy sources mitigate climate change by providing people with energy not derived from the combustion of fossil fuels. Finally, simple activities such as energy conservation, choosing to walk or bike instead of driving, and disposing of waste properly are activities that, when done by large numbers of people, actively mitigate climate change by preventing carbon emissions.

Video



This 2-minute video describes using natural and artificial carbon sinks to help mitigate climate change but notes that these do not solve it.
Question after watching: What is the ultimate solution to mitigating climate change?

? Optional Activity 24.4.1

Why are forests important for mitigating climate change?

A. Forests serve as a sink in the carbon cycle.
B. Trees provide building materials.
C. Trees are an important food source.
D. Leaves of trees reflect all sunlight away from the Earth.

Answer

A. Forests serve as a sink in the carbon cycle.

Climate Adaptation Strategies

Beyond mitigation, we know that climate change is already occurring as we can see and feel its effects. For this reason, it is essential to also adapt to our changing environment. This means that we must change our behaviors in response to the changing environment around us. Adaptation strategies will vary greatly by region, depending on the largest specific impacts in that area. For example, in the city of Delhi, India, a dramatic decrease in rainfall is projected over the next century. This city will likely need to implement policies and practices relating to the conservation of water like rainwater harvesting, water re-use, and increased irrigation efficiency. Rain-limited cities near oceans, such as Los Angeles, California may choose to use desalination to provide drinking water to their citizens. **Desalination** involves taking the salt out of seawater to make it potable. Cities with low elevations near oceans may need to implement adaptation strategies to rising sea levels, from seawalls and levees to relocation of citizens. One adaptation strategy gaining use is the creation or conservation of wetlands, which provide natural protection against storm surges and flooding.

The IPCC 6th Assessment Report (2022) outlines just some of the following global strategies for adaptation to climate change:

- Sustainable land use and urban planning
- Water use efficiency and water resource management
- Integrated coastal zone management
- Resilient power systems
- Health and health systems adaptation
- Planned relocation and resettlement
- Disaster risk management
- Climate services, including Early Warning Systems

Want to know more? Visit this site for short courses on Climate Change Adaptation Fundamentals: https://pcs.royalroads.ca/climate-change-adaptation-fundamentals-online

Indigenous Connections: Climate Action



In Canada, British Columbia's climate is changing, and Indigenous peoples are taking action to help their communities prepare and adapt to these impacts. In this 5-minute video, some actions are highlighted including helping the Klinse-Za caribou thrive in a new environment, adapting traditional food systems at T'eqt"aqutn'mux and Fort Nelson First Nation returning to fish camp.

Question after watching: Which of the adaptation measures listed above did you see in the video?

If we are to mitigate and adapt to the far-reaching impacts of climate change, we must carefully monitor and study changes in biological communities and ecosystem functioning, and how they relate to changes in climate and other stressors. While we may lose some species in a warmer world, we can also prevent many extinctions with proactive wildlife management. It is likely that many existing protected areas will no longer preserve some of the rare and threatened species that currently live in them, necessitating careful planning when establishing new protected areas. Even if climate change is not as severe as predicted, the steps we take now to safeguard biodiversity and our own future can only help.

Summary

1. While climate change is often thought of as a future challenge, we can already see its impacts today, as shown by record-high temperatures and changing rainfall patterns. These changes are happening because human activities release large amounts of greenhouse gases into the atmosphere on a daily basis.
2. Habitat loss contributes to climate change directly through the destruction of complex ecosystems (i.e. carbon sinks) which releases stored CO_2, and indirectly through the loss of vegetation that would otherwise sequester CO_2 from the atmosphere.
3. Some climatic shifts are predicted to be so rapid in the coming decades that many species will be unable to adjust their ranges to keep up with environmental changes. Species with dispersal limitations, special habitat requirements, and important mutualistic relationships are at an especially high risk of extinction.
4. Species are seldom exposed to only one threat; rather, different threats interact with climate change so that their combined impact is greater than their individual effects. A successful conservation strategy needs to deal with these threats collectively.
5. Mitigating the negative impacts of climate change will require an international multi-pronged approach that includes ecosystem protection and restoration, direct species management, and legislative action.

Optional Resources:

- US Global Change Research Program
- Individual actions (via EPA)
- UN's 2022 Conference of the Parties 27th Annual Meeting (COP 27)
- Intergovernmental Panel on Climate Change
- 10 Solutions to Climate Change (Scientific American)

Video



In the lead-up to the largest climate mobilization in history (the Climate March of 2014), this documentary weaves together the science, politics, and psychology of humanity's collective inaction to address the greatest ecological, social, and moral challenge of our time.

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