PRINCIPLES OF ECOLOGY



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Principles of Ecology

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1.1: INTRODUCTION TO BIOLOGY

Viewed from space, Earth offers no clues about the diversity of life forms that reside there. Scientists believe that the first forms of life on Earth were microorganisms that existed for billions of years in the ocean before plants and animals appeared. The mammals, birds, and flowers so familiar to us are all relatively recent, originating 130 to 250 million years ago. The earliest representatives of the genus *Homo*, to which we belong, have inhabited this planet for only the last 2.5 million years, and only in the last 300,000 years have humans started looking like we do today.



Figure 1.1 This NASA image is a composite of several satellite-based views of Earth. To make the whole-Earth image, NASA scientists combine observations of different parts of the planet. (credit: NASA/GSFC/NOAA/USGS)

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SECTION OVERVIEW

1.2: Introduction to Ecology



An earth star fungus, *Geastrum* aff. *welwitschii*. The strange structures shown are but a small part of the fungus, developed by that organism under genetic control to produce and disperse its spores. Much more of the biomass of this life form is found within the soil.

The objective of this wikibook, *A Study Guide to Basic Ecology*, is to give the reader a better understanding of the way life functions on Earth, and how it is organized. This section will introduce basic concepts and definitions required to establish a course that is both biological and ecological in approach. You will learn that there are numerous terms in ecology which basically mean the same thing, and that there are also a plethora of views on precise definitions. As ecology emerged in the 19th and early 20th centuries, many concepts of ecological organization were proposed. These came from both zoologists and botanists—whom seldom read the other's literature—and from different schools of thought.

Definition of Ecology

The term ***oekologie*** (ecology) was coined in 1866 by the German biologist, Ernst Haeckel from the Greek *oikos* meaning "house" or "dwelling", and *logos* meaning "science" or "study". Thus, ecology is the "study of the household of nature". Haeckel intended it to encompass the study of an animal in relation to both the physical environment and other plants and animals with which it interacted.

A contemporary definition of ecology is:

The scientific study of the distribution and abundance of organisms and the interactions that determine distribution and abundance[1].

This definition encompasses not only the plants and animals that Haeckel recognized but microscopic organisms such as Bacteria, Archaea and protozoa, as well. The interactions that determine an organism's distribution and abundance are processes that include energy flow, growth, reproduction, predation, competition and many others. [2]



Ecology is essentially the study of the workings of the planet Earth.

To fully understand the science of ecology, there are some common terms that must be defined. The term **environment** describes, in an unspecified way, the sum total of physical and biotic conditions that influence an organism (Kendeigh, 1961). The subset of the planet earth *environment* into which life penetrates is termed the **biosphere**. With respect to the planet earth, the biosphere penetrates only a limited distance into the rock beneath the land and the oceans, and a limited distance out away from the planet towards space. All human effort so far has failed to demonstrate that the biosphere extends beyond these limits or that other biospheres exist elsewhere in the universe. We cannot therefore conclude that they do not exist, only that we know nothing of that existence. **Ecosystem** is perhaps the most widely used term in ecology. It is defined as the system of organisms and physical factors under study or consideration. Although the boundaries of ecosystems are sometimes quite difficult to define in nature, ecosystems —however bounded—comprise the basic units of that nature (Tansley, 1935). **Habitat** is generally considered by biologists to be the physical conditions that surround a species, or species population, or assemblage of species, or community (Clements and Shelford, 1939).

The basic physical units of the biosphere are the **lithosphere** (the land), **hydrosphere** (the water), and **atmosphere** (the air). Apparently there is no permanent biota of the atmosphere, although insects and birds among others utilize that environment extensively (Hesse, et al., 1951). These basic units are easily recognized in any **landscape**, as for example shown in the scene at right from Belarus in Europe.

- Read Biosphere (Follow links that interest you. Most subtopics will be covered in later chapters)
- Read Ecosystem (Links need only be followed to deepen your interest at this time)

Note

Definitions of terms used in this textbook have been collected into various glossaries, the basic one being Basic Ecology Glossary.



Tropical woodlands and River Gambia. The surface of the earth is covered by an exceedingly complex biological system capturing energy from sunlight. Availability of water determines the "density" of this system.

Humanity has been studying nature for thousands of years and formally for several centuries under the science of biology, so why do we say that Ecology is a relatively new science? (Note, the term "ecology" is only about 150 years old). What is it that ecologists do or study that biologists might not? Kendeigh (1961, p. 3) wrote that "[e]cology is one of three main divisions of biology; the other two being morphology [organism structural aspects] and physiology [organism functional aspects]". The behavioral sciences encompass one facet of the interaction of an organism with its physical and biological surroundings, and therefore are part of ecology.

Several techniques are used to study Ecology; one of the methods is known as strong inference. Strong inference is defined as the method of testing a hypothesis by deliberately attempting to demonstrate the falsity of the hypothesis (Kinraide and Denison, 2003). Performing experiments is the preferred method of using strong inference. The point of an experiment is to control variables and/or patterns and to predict the outcomes.

Traditionally, Ecology is based more on weak inference (the other type of inference) rather than strong inference. In weak inference there are no experiments; rather, there are correlations between observations. Weak inference is defined as a "common sense" approach using simple system models to build understanding (Elner and Vadas).

Both weak and strong inference have been used throughout many different science courses over the last several thousands of years (Kinraide and Denison). However, strong inference is said to be more advantageous because weak inference is more prone to error. Weak inference makes people try to cling to one point of view; whereas strong inference (doing experimentation) causes people to think from more than one point of view and keep coming up with different hypotheses to test as their old hypotheses get falsified.

Ecology incorporates and overlaps with many other disciplines in both the biological and physical sciences. Certainly on one level, there is no information about the natural environment that does not have some applicability to ecology. On the other hand, such interrelationships between the sciences are much more the norm than most people realize. Ecology, according to Kendeigh (1961, p. 1), is a distinct science because of the way information about the natural world is organized; and because of its unique methodologies and point-of-view by which knowledge is extracted from such information.

> *Ecology has no aim, but ecologists have. The problems of the ecologist are not fundamentally different from those of any other kind of naturalist. The superficial differences in aim are due to the different points of view, or methods of approach, rather than to any essential differences in the character of the problems* — (Charles Adams, 1913; cited in Hedgepeth, 1957).

It may be helpful here to list the phenomenon that ecologists are particularly interested in if only to better clarify the boundaries of this text covering basic ecology (list modified from Kendeigh, 1961, p 1). Ecologists study:

1. structural, functional, and behavioral adaptations of organisms in relation to their environment (Chapter 3);
2. interrelationships between species and their populations, and populations in their communities (Chapter 4);
3. local and geographic distributions of organisms;
4. regional variations in organism abundances;
5. temporal changes in the distribution, abundance, and behaviors of organisms; and

6. evolution of the interrelationships described.

Ecology is both a biological and an environmental science, something that should certainly be evident from the definition provided above. Many environmental sciences are minimally concerned with biology (meteorology, for example) and others (environmental toxicology, for example) necessarily combine physical and biological sciences. Environmentalism on the other hand is a political position involved with various aspects of managing the environment.

- Read Ecology (Neither links nor extended ("Main") articles need be pursued at this time)

There are many subcategories of Ecology. Plant Ecology looks at the differences and similarities of various plants in differing climates and habitats. The origins of Animal Ecology can be traced to two Europeans, R. Hesse of Germany and Charles Elton of England . Physiological Ecology, or ecophysiology, studies the responses of the individual organism to the environment. The idea of Population Ecology was brought forward by two famous men, Charles Darwin, who looked at the similarities and dissimilarities of populations and how they replaced each other over time, and Gregor Mendel . The last subcategory is Ecosystem Ecology, which brought about terms such as limnology, introduced by A. Thienemann.

Early History of Ecology

Because ecology is a facet of biology, it is not possible to clearly define a time or person that represents the beginning of ecological thought as distinct from biology. One of the first ecologists was probably Theophrastus, a contemporary and student of Aristotle. Theophrastus described various interrelationships between animals and between animals and their environment as early as the 4th century BC (Ramalay, 1940).

- Read Theophrastus (Links need not be pursued at this time except as necessary to clarify points)

Over the next several centuries biological knowledge gradually expanded as naturalists, such as Bufon and Linnaeus, contributed to a growing understanding of the nature of plants and animals. These early naturalists of course understood that organisms had a relationship with the environment, and especially that the distribution of forms was related to physical aspects of the geography.

- Read Carolus Linnaeus (Follow links only as needed to clarify terms and points made)
- Read Alexander von Humboldt (Follow links only as needed to clarify terms and points made)

The modern ecological concept of integrated communities of organisms began in the 19th century with the studies of August Grisebach (1838), a German botanist. A contemporary and fellow countryman, Ernst Haeckel, coined the term "ecology" in 1866. Other biologists followed Grisbach's ecological approach to natural history studies: K. Möbius (1877) investigating Danish oyster banks, Stephen A. Forbes (1887), describing a lake community as a microcosm, J. E. B. Warming (1895), describing Danish plant communities, and C. C. Adams conducting ecological stuidies in northern Michigan (1905) and at Isle Royale (1909).

- Read Ernst Haeckel (Follow links only as needed to clarify terms and points made)
- Read History of Ecology (Pursue only links that interest you to gain additional insight)

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1.3: THE SCIENCE OF BIOLOGY

LEARNING OBJECTIVES

By the end of this section, you will be able to do the following:

- Identify the shared characteristics of the natural sciences
- Summarize the steps of the scientific method
- Compare inductive reasoning with deductive reasoning
- Describe the goals of basic science and applied science

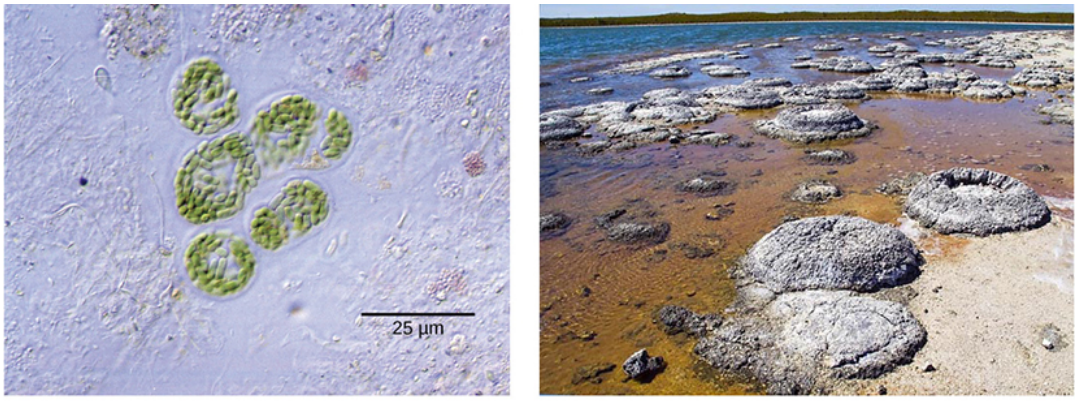


Figure 1.2 Formerly called blue-green algae, these (a) cyanobacteria, magnified 300x under a light microscope, are some of Earth's oldest life forms. These (b) stromatolites along the shores of Lake Thetis in Western Australia are ancient structures formed by layering cyanobacteria in shallow waters. (credit a: modification of work by NASA; credit b: modification of work by Ruth Ellison; scale-bar data from Matt Russell)

What is biology? In simple terms, biology is the study of life. 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 1.2). Listening to the daily news, you will quickly realize how many aspects of biology we discuss every day. For example, recent news topics include *Escherichia coli* (Figure 1.3) 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.

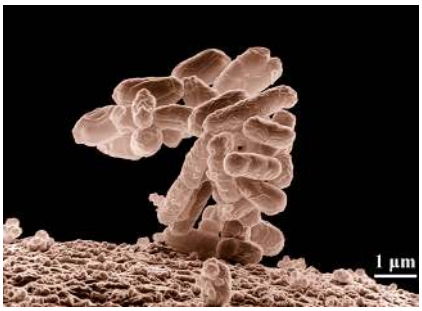


Figure 1.3 *Escherichia coli* (*E. coli*) bacteria, in this scanning electron micrograph, are normal residents of our digestive tracts that aid in absorbing vitamin K and other nutrients. However, virulent strains are sometimes responsible for disease outbreaks. (credit: Eric Erbe, digital colorization by Christopher Pooley, both of USDA, ARS, EMU)

THE PROCESS OF SCIENCE

Biology is a science, but what exactly is science? What does the study of biology share with other scientific disciplines? We can define science (from the Latin *scientia*, meaning "knowledge") as knowledge that covers general truths or the operation of general laws, especially when acquired and tested by the scientific method. It becomes clear from this definition that applying scientific method plays a major role in science. The scientific method is a method of research with defined steps that include experiments and careful observation.

We will examine scientific method steps 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 one can test. Although using the scientific method is inherent to science, it is inadequate in determining what science is. This is because it is relatively easy to apply the scientific method to disciplines such as physics and chemistry, but when it comes to disciplines like archaeology, psychology, and geology, the scientific method becomes less applicable as repeating experiments becomes more difficult.

These areas of study are still sciences, however. Consider archaeology—even though one cannot perform repeatable experiments, hypotheses may still be supported. For instance, archaeologists can hypothesize that an ancient culture existed based on finding a piece of pottery. They could make further hypotheses about various characteristics of this culture, which could be correct or false through continued support or contradictions from other findings. A hypothesis may become a verified theory. A theory is a tested and confirmed explanation for observations or phenomena. Therefore, we may be better off to define science as fields of study that attempt to comprehend the nature of the universe.

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? Maybe all of the above? Science includes such diverse fields as astronomy, biology, computer sciences, geology, logic, physics, chemistry, and mathematics (Figure 1.4). However, scientists consider those fields of science related to the physical world and its phenomena and processes natural sciences. Thus, a museum of natural sciences might contain any of the items listed above.

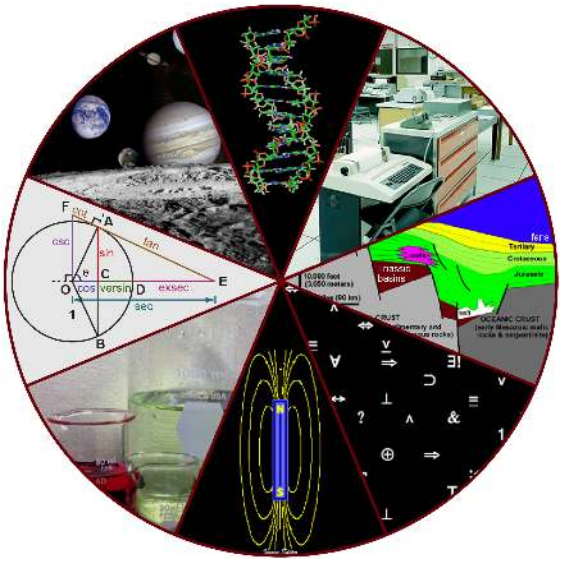


Figure 1.4 The diversity of scientific fields includes astronomy, biology, computer science, geology, logic, physics, chemistry, mathematics, and many other fields. (credit: “Image Editor”/Flickr)

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. Some refer to natural sciences as “hard science” because they rely on the use of quantitative data. Social sciences that study society and human behavior are more likely to use qualitative assessments to drive investigations and 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.

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.

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 one can supplement the raw data 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 analyzing a large amount of data. Brain studies provide an example. In this type of research, scientists observe many live brains while people are engaged in a specific activity, such as viewing images of food. The scientist then predicts the part of the brain that "lights up" during this activity to be the part controlling the response to the selected stimulus, in this case, images of food. Excess absorption of radioactive sugar derivatives by active areas of the brain causes the various areas to "light up". Scientists use a scanner to observe the resultant increase in radioactivity. 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 reasoning, 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 predict specific results. From those general principles, a scientist can deduce 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.

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, while hypothesis-based science, which is usually deductive, begins with a specific question or problem and a potential answer or solution that one can test. The boundary between these two forms of study is often blurred, and most scientific endeavors combine both approaches. 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 experimented to find the best material that acted similarly, 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. Known as scientific method, this approach is common to other sciences as well. The scientific method was used even in ancient times, but England's Sir Francis Bacon (1561–1626) first documented it (Figure 1.5). He set up inductive methods for scientific inquiry. The scientific method is not used only by biologists; researchers from almost all fields of study can apply it as a logical, rational problem-solving method.



Figure 1.5 Historians credit Sir Francis Bacon (1561–1626) as the first to define the scientific method. (credit: Paul van Somer)

The scientific process typically starts with an observation (often a problem to solve) 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?"

PROPOSING A HYPOTHESIS

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

Once one has selected a hypothesis, 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."

TESTING A HYPOTHESIS

A valid hypothesis must be testable. It should also be falsifiable, meaning that experimental results can disprove it. 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 every feature of the experimental group except it is not given the manipulation that the researcher hypothesizes. Therefore, if the experimental group's results differ from the control group, the difference must be due to the hypothesized manipulation, rather than some outside factor. Look for the variables and controls in the examples that follow. 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 the student should reject this hypothesis. 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 the student should reject this hypothesis. The students should test each hypothesis by carrying out appropriate experiments. Be aware that rejecting one hypothesis does not determine whether or not one can accept the other hypotheses. It simply eliminates one hypothesis that is not valid (Figure 1.6). Using the scientific method, the student rejects the hypotheses that are inconsistent with experimental data.

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.

In hypothesis-based science, researchers predict specific results from a general premise. We call this type of reasoning deductive reasoning: deduction proceeds from the general to the particular. However, the reverse of the process is also possible: sometimes, scientists reach a general conclusion from a number of specific observations. We call this type of reasoning inductive reasoning, and it proceeds from the particular to the general. Researchers often use inductive and deductive reasoning in tandem to advance scientific knowledge (Figure 1.7). In recent years a new approach of testing hypotheses has developed as a result of an exponential growth of data deposited in various databases. Using computer algorithms and statistical analyses of data in databases, a new field of so-called "data research" (also referred to as "in silico" research) provides new methods of data analyses and their interpretation. This will increase the demand for specialists in both biology and computer science, a promising career opportunity.

VISUAL CONNECTION

VISUAL CONNECTION

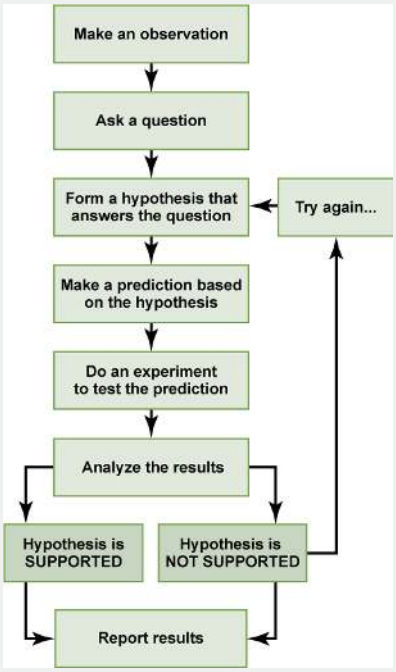


Figure 1.6 The scientific method consists of a series of well-defined steps. If a hypothesis is not supported by experimental data, one can propose a new hypothesis.

In the example below, the scientific method is used to solve an everyday problem. Match 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	a. There is something wrong with the electrical outlet.
2. Question	b. If something is wrong with the outlet, my coffeemaker also won't work when plugged into it.
3. Hypothesis (answer)	c. My toaster doesn't toast my bread.
4. Prediction	d. I plug my coffee maker into the outlet.
5. Experiment	e. My coffeemaker works.
6. Result	f. Why doesn't my toaster work?

VISUAL CONNECTION

VISUAL CONNECTION

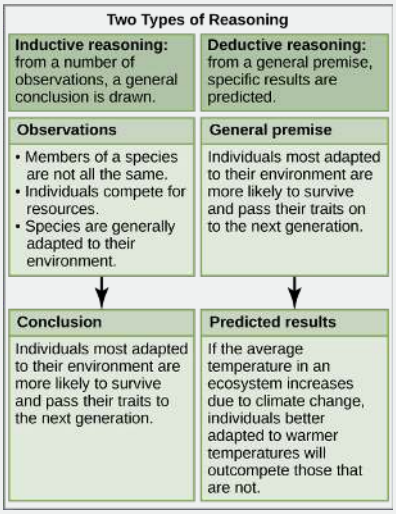


Figure 1.7 Scientists use two types of reasoning, inductive and deductive reasoning, to advance scientific knowledge. As is the case in this example, the conclusion from inductive reasoning can often become the premise for deductive reasoning.

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, are distributed evenly between the daughter cells during cell division. Therefore, each daughter cell will have the same chromosome set as the mother cell.
4. Animals as diverse as humans, insects, and wolves all exhibit social behavior. Therefore, social behavior must have an evolutionary advantage.

The scientific method may seem too rigid and structured. It is important to keep in mind that, although scientists often follow this sequence, there is flexibility. 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 we can apply the scientific method to solving problems that aren't necessarily scientific in nature.

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, although 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 1.8). In applied science, the problem is usually defined for the researcher.



Figure 1.8 After Hurricane Irma struck the Caribbean and Florida in 2017, thousands of baby squirrels like this one were thrown from their nests. Thanks to applied science, scientists knew how to rehabilitate the squirrel. (credit: audreyjm529, Flickr)

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?” However, a careful look at the history of science 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 researchers develop an application, therefore, applied science relies on the results that researchers generate through basic science. Other scientists think that it is time to move on from basic science in order to find solutions to actual problems. Both approaches are valid. It is true that there are problems that demand immediate attention; however, scientists would find few solutions without the help of the wide knowledge foundation that basic science generates.

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. DNA strands, unique in every human, are in our cells, where they provide the instructions necessary for life. When DNA replicates, it produces new copies of itself, shortly before a cell divides. Understanding DNA replication mechanisms enabled scientists to develop laboratory techniques that researchers now use to identify genetic diseases, pinpoint individuals who were at a crime scene, and determine paternity. Without basic science, it is unlikely that applied science could exist.

Another example of the link between basic and applied research is the Human Genome Project, a study in which researchers analyzed and mapped each human chromosome to determine the precise sequence of DNA subunits and each gene's exact location. (The gene is the basic unit of heredity represented by a specific DNA segment that codes for a functional molecule. An individual’s complete collection of genes is their genome.) Researchers have studied other less complex organisms as part of this project in order to gain a better understanding of human chromosomes. The Human Genome Project (Figure 1.9) relied on basic research with simple organisms and, later, with the human genome. An important end goal eventually became using the data for applied research, seeking cures and early diagnoses for genetically related diseases.

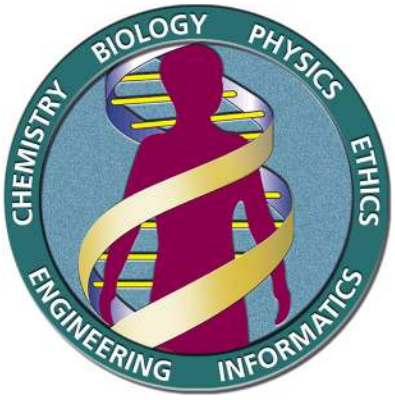


Figure 1.9 The Human Genome Project was a 13-year collaborative effort among researchers working in several different science fields. Researchers completed the project, which sequenced the entire human genome, in 2003. (credit: the U.S. Department of Energy Genome Programs (http://genomics.energy.gov)

While scientists usually carefully plan research efforts in both basic science and applied science, note that some discoveries are made by serendipity, that is, by means of a fortunate accident or a lucky surprise. Scottish biologist Alexander Fleming discovered penicillin when he

accidentally left a petri dish of *Staphylococcus* bacteria open. An unwanted mold grew on the dish, killing the bacteria. Fleming's curiosity to investigate the reason behind the bacterial death, followed by his experiments, led to the discovery of the antibiotic penicillin, which is produced by the fungus *Penicillium*. Even in the highly organized world of science, luck—when combined with an observant, curious mind—can lead to unexpected breakthroughs.

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—is 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 a scientist's colleagues or peers review. 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 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.

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 must be brief, 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 also briefly mentions the end of the paper, where the researcher will present the hypothesis or research question driving the research. 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 plagiarism.

The materials and methods section includes a complete and accurate description of the substances the researchers use, and the method and techniques they use 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 the researchers made measurements and the types of calculations and statistical analyses they 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 it is more common to combine both. If the journal does not allow combining both sections, the results section simply narrates the findings without any further interpretation. The researchers present results with tables or graphs, but they do not present duplicate information. In the discussion section, the researchers 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, researchers include proper citations in this section as well.

Finally, the conclusion section summarizes the importance of the experimental findings. While the scientific paper almost certainly answers one or more scientific questions that the researchers stated, any good research should lead to more questions. Therefore, a well-done scientific paper allows the researchers 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.

SCIENTIFIC ETHICS

Scientists must ensure that their efforts do not cause undue damage to humans, animals, or the environment. They also must ensure that their research and communications are free of bias and that they properly balance financial, legal, safety, replicability, and other considerations. All scientists -- and many people in other fields -- have these ethical obligations, but those in the life sciences have a particular obligation because their research may involve people or other living things. Bioethics is thus an important and continually evolving field, in which researchers collaborate with other thinkers and organizations. They work to define guidelines for current practice, and also continually consider new developments and emerging technologies in order to form answers for the years and decades to come.

For example, bioethicists may examine the implications of gene editing technologies, including the ability to create organisms that may displace others in the environment, as well as the ability to “design” human beings. In that effort, ethicists will likely seek to balance the positive outcomes -- such as improved therapies or prevention of certain illnesses -- with negative outcomes.

Unfortunately, the emergence of bioethics as a field came after a number of clearly unethical practices, where biologists did not treat research subjects with dignity and in some cases did them harm. In the 1932 Tuskegee syphilis study, 399 African American men were diagnosed with syphilis but were never informed that they had the disease, leaving them to live with and pass on the illness to others. Doctors even withheld proven medications because the goal of the study was to understand the impact of untreated syphilis on Black men.

While the decisions made in the Tuskegee study are unjustifiable, some decisions are genuinely difficult to make. Bioethicists work to establish moral and dignifying approaches before such decisions come to pass. For example, doctors rely on artificial intelligence and robotics for medical diagnosis and treatment; in the near future, even more responsibility will lie with machines. Who will be responsible for medical decisions? Who will explain to families if a procedure doesn’t go as planned? And, since such treatments will likely be expensive, who will decide who has access to them and who does not? These are all questions bioethicists seek to answer, and are the types of considerations that all scientific researchers take into account when designing and conducting studies.

Bioethics are not simple, and often leave scientists balancing benefits with harm. In this text and course, you will discuss medical discoveries, vaccines, and research that, at their core, have an ethical complexity or, in the view of many, an ethical lapse. In 1951, Henrietta Lacks, a 30-year-old African American woman, was diagnosed with cervical cancer at Johns Hopkins Hospital. Unique characteristics of her illnesses gave her cells the ability to divide continuously, essentially making them “immortal.” Without her knowledge or permission, researchers took samples of her cells and with them created the immortal HeLa cell line. These cells have contributed to major medical discoveries, including the polio vaccine. Many researchers mentioned in subsequent sections of the text relied on HeLa cell research as at least a component of their work related to cancer, AIDS, cell aging, and even very recently in COVID-19 research.

Today, harvesting tissue or organs from a dying patient without consent is not only considered unethical but illegal, regardless of whether such an act could save other patients’ lives. Is it ethical, then, for scientists to continue to use Lacks’s tissues for research, even though they were obtained illegally by today’s standards? Should Lacks be mentioned as a contributor to the research based on her cells, and should she be cited in the several Nobel Prizes that have been awarded through such work? Finally, should medical companies be obligated to pay Lacks’ family (which had financial difficulties) a portion of the billions of dollars in revenue earned through medicines that benefited from HeLa cell research? How would Henrietta Lacks feel about this? Because she was never asked, we will never know.

To avoid such situations, the role of ethics in scientific research is to ask such questions before, during, and after research or practice takes place, as well as to adhere to established professional principles and consider the dignity and safety of all organisms involved or affected by the work.

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1.4: THEMES AND CONCEPTS OF BIOLOGY

LEARNING OBJECTIVES

By the end of this section, you will be able to do the following:

- Identify and describe the properties of life
- Describe the levels of organization among living things
- Recognize and interpret a phylogenetic tree
- List examples of different subdisciplines in 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. 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: What are the shared properties that make something “alive”? Once we know something is alive, how do we find meaningful levels of organization in its structure? 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 scientists discover new organisms every day, biologists continue to seek answers to these and other questions.

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 eight characteristics serve to define life.

ORDER



Figure 1.10 A toad represents a highly organized structure consisting of cells, tissues, organs, and organ systems. (credit: “Ivengo”/Wikimedia Commons)

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 comprise molecules. These in turn comprise cell organelles and other cellular inclusions. In multicellular organisms (Figure 1.10), similar cells form tissues. Tissues, in turn, collaborate to create organs (body structures with a distinct function). Organs work together to form organ systems.

SENSITIVITY OR RESPONSE TO STIMULI



Figure 1.11 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)

Organisms respond to diverse stimuli. For example, plants can bend toward a source of light, climb on fences and walls, or respond to touch (Figure 1.11). Even tiny bacteria can move toward or away from chemicals (a process called *chemotaxis*) or light (*phototaxis*). Movement toward a stimulus is a positive response, while movement away from a stimulus is a negative response.

LINK TO LEARNING

LINK TO LEARNING

Watch this video to see how plants respond to a stimulus—from opening to light, to wrapping a tendril around a branch, to capturing prey.

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 cells—gametes and oocyte and sperm cells. After fertilization (the fusion of an oocyte and a sperm cell), a new individual develops. When reproduction occurs, DNA containing genes 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.

ADAPTATION

All living organisms exhibit a "fit" to their environment. Biologists refer to this fit as adaptation, and it is a consequence of evolution by natural selection, which operates in every lineage of reproducing organisms. Examples of adaptations are diverse and unique, from heat-resistant Archaea that live in boiling hotsprings to the tongue length of a nectar-feeding moth that matches the size of the flower from which it feeds. Adaptations enhance the reproductive potential of the individuals exhibiting them, including their ability to survive to reproduce. Adaptations are not constant. As an environment changes, natural selection causes the characteristics of the individuals in a population to track those changes.

GROWTH AND DEVELOPMENT

Organisms grow and develop as a result of genes providing specific instructions that will direct cellular growth and development. This ensures that a species' young (Figure 1.12) will grow up to exhibit many of the same characteristics as its parents.



Figure 1.12 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/HOMEOSTASIS

Even the smallest organisms are complex and require multiple regulatory mechanisms to coordinate internal functions, respond to stimuli, and cope with environmental stresses. Homeostasis (literally, "steady state") refers to the relatively stable internal environment required to maintain life. 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.



Figure 1.13 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)

In order to function properly, cells require 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 homeostatic internal conditions within a narrow range almost constantly, despite environmental changes, by activation of regulatory mechanisms. For example, an organism needs to regulate body temperature through the thermoregulation process. Organisms that live in cold climates, such as the polar bear (Figure 1.13), 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.

ENERGY PROCESSING



Figure 1.14 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)

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 1.14).

EVOLUTION

The diversity of life on Earth is a result of mutations, or random changes in hereditary material over time. These mutations allow the possibility for organisms to adapt to a changing environment. An organism that evolves characteristics fit for the environment will have greater reproductive success, subject to the forces of natural selection.

LEVELS OF ORGANIZATION OF LIVING THINGS

Living things are highly organized and structured, following a hierarchy that we can examine on a scale from small to large. The atom is the smallest and most fundamental unit of matter that retains the properties of an element. 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 1.15), which contains the instructions for the structure and functioning of all living organisms.

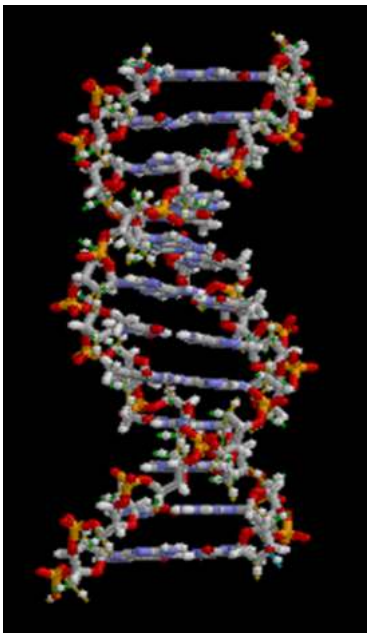


Figure 1.15 All molecules, including this DNA molecule, are comprised of atoms. (credit: “brian0918”/Wikimedia Commons)

LINK TO LEARNING

LINK TO LEARNING

Watch this video that animates the three-dimensional structure of the DNA molecule in Figure 1.15.

Some cells contain aggregates of macromolecules surrounded by membranes. We call these 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 scientists do not consider viruses 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. Scientists classify cells 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 organisms, which biologists typically call microorganisms.

Biologists collectively call all the individuals of a species living within a specific area a population. For example, a forest may include many pine trees, which represent the population of pine trees in this forest. Different populations may live in the same specific area. For example, the forest with the pine trees includes populations of flowering plants, 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, nonliving parts of that environment such as nitrogen in the soil or rain water. At the highest level of organization (Figure 1.16), the biosphere is the collection of all ecosystems, and it represents the zones of life on Earth. It includes land, water, and even the atmosphere to a certain extent.

VISUAL CONNECTION

VISUAL CONNECTION

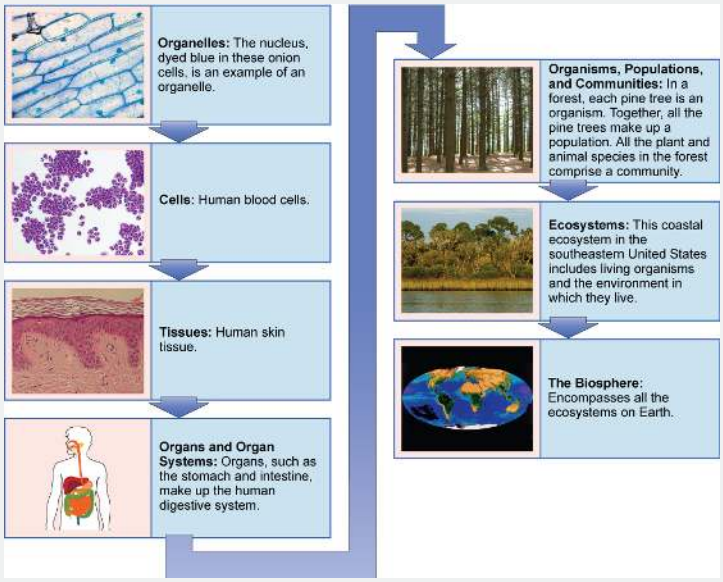


Figure 1.16 shows the biological levels of organization of living things. From a single organelle to the entire biosphere, living organisms are parts of a highly structured hierarchy. (credit “organelles”: modification of work by Umberto Salvagnin; credit “cells”: modification of work by Bruce Wetzel, 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)

Which of the following statements is false?

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.

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 in a population or species over time. Evolutionary biologists study the evolution of living things in everything from the microscopic world to ecosystems.

A phylogenetic tree (Figure 1.17) can summarize the evolution of various life forms on Earth. It is a diagram showing the evolutionary relationships among biological species based on similarities and differences in genetic or physical traits or both. Nodes and branches comprise a phylogenetic tree. The internal nodes represent ancestors and are points in evolution when, based on scientific evidence, researchers believe an ancestor has diverged to form two new species. The length of each branch is proportional to the time elapsed since the split.

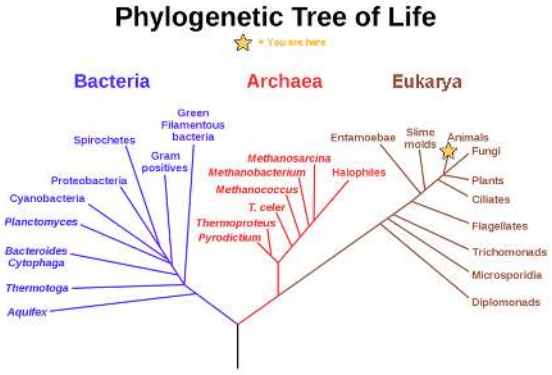


Figure 1.17 Microbiologist Carl Woese constructed this phylogenetic tree using data that he obtained from sequencing ribosomal RNA genes. The tree shows the separation of living organisms into three domains: Bacteria, Archaea, and Eukarya. Bacteria and Archaea are

prokaryotes, single-celled organisms lacking intracellular organelles. (credit: Eric Gaba; NASA Astrobiology Institute)

EVOLUTION CONNECTION

EVOLUTION CONNECTION

Carl Woese and the Phylogenetic TreeIn the past, biologists grouped living organisms into five kingdoms: animals, plants, fungi, protists, and bacteria. They based the organizational scheme mainly on physical features, as opposed to physiology, biochemistry, or molecular biology, all of which modern systematics use. American microbiologist Carl Woese's pioneering work 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 (protists), together with the three remaining kingdoms (fungi, plants, and animals). Woese defined Archaea as a new domain, and this resulted in a new taxonomic tree (Figure 1.17). 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 constructed his tree from universally distributed comparative gene sequencing that are present in every organism, and conserved (meaning that these genes have remained essentially unchanged throughout evolution). Woese's approach was revolutionary because comparing physical features are insufficient to differentiate between the prokaryotes that appear fairly similar in spite of their tremendous biochemical diversity and genetic variability (Figure 1.18). Comparing rRNA sequences provided Woese with a sensitive device that revealed the extensive variability of prokaryotes, and which justified separating the prokaryotes into two domains: bacteria and archaea.

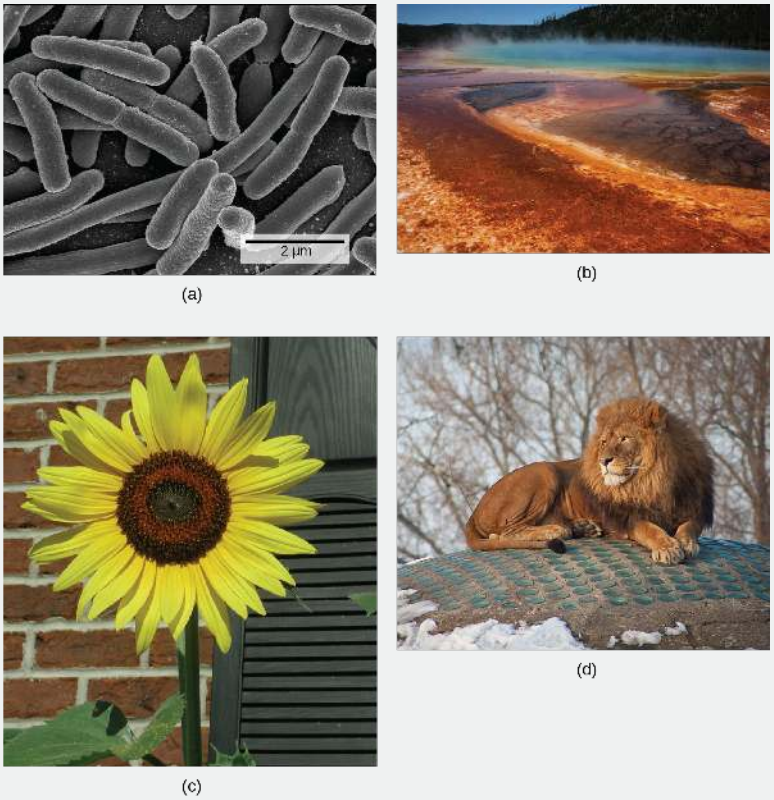


Figure 1.18 These images represent different domains. The (a) bacteria in this micrograph belong to Domain Bacteria, while the (b) extremophiles (not visible) living in this hot vent belong to Domain Archaea. Both the (c) sunflower and (d) lion are part of Domain Eukarya. (credit a: modification of work 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 itself, and depending on the subject of study, there are also microbial physiologists, ecologists, and geneticists, among others.

CAREER CONNECTION

CAREER CONNECTION

Forensic ScientistForensic science is the application of science to answer questions related to the law. Biologists as well as chemists and biochemists can be forensic scientists. Forensic scientists provide scientific evidence for use in courts, and their job involves examining trace materials associated with crimes. Interest in forensic science has increased in the last few years, possibly because of popular television shows that feature forensic scientists on the job. Also, developing molecular techniques and establishing DNA databases have expanded the types of work that forensic scientists can do. Their job activities are primarily related to crimes against people such as murder, rape, and assault. Their work involves analyzing samples such as hair, blood, and other body fluids and also processing DNA (Figure 1.19) found in many different environments and materials. Forensic scientists also analyze other biological evidence left at crime scenes, such as insect larvae or pollen grains. Students who want to pursue careers in forensic science will most likely have to take chemistry and biology courses as well as some intensive math courses.



Figure 1.19 This forensic scientist works in a DNA extraction room at the U.S. Army Criminal Investigation Laboratory at Fort Gillem, GA. (credit: United States Army CID Command Public Affairs)

Another field of biological study, neurobiology, studies the biology of the nervous system, and although it is a branch of biology, it is also an interdisciplinary field of study known as neuroscience. Because of its interdisciplinary nature, this subdiscipline studies different nervous system functions using molecular, cellular, developmental, medical, and computational approaches.



Figure 1.20 Researchers work on excavating dinosaur fossils at a site in Castellón, Spain. (credit: Mario Modesto)

Paleontology, another branch of biology, uses fossils to study life's history (Figure 1.20). Zoology and botany are the study of animals and plants, respectively. Biologists can also specialize as biotechnologists, ecologists, or physiologists, to name just a few areas. This is just a small sample of the many fields that biologists can pursue.

Biology is the culmination of the achievements of the natural sciences from their inception to today. Excitingly, it is the cradle of emerging sciences, such as the biology of brain activity, genetic engineering of custom organisms, and the biology of evolution that uses the laboratory tools of molecular biology to retrace the earliest stages of life on Earth. A scan of news headlines—whether reporting on immunizations, a newly discovered species, sports doping, or a genetically-modified food—demonstrates the way biology is active in and important to our everyday world.

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SECTION OVERVIEW

1.5: Ecological Organization

Units of the Biosphere

You have been presented with a definition of the term **biosphere** above. This chapter will consider the question: **How is the *biosphere* organized?** We will initially look at this organization over a range of scales so to familiarize you to important terms used in ecology. In later chapters, we will cover the details and significance of the concepts only introduced here.



A large pond and wetlands near Minsk. We can easily recognize a hydrosphere, an atmosphere, and a lithosphere, the latter dominated in some areas by yellowing grasses or sedges, in other areas by trees.

Ecologists regard *ecosystems* as basic structural units, implying that the biosphere is a collection or mosaic of definable ecosystems. However, an ecosystem is really more conceptual than actual. By this we mean that the definable boundaries of an ecosystem are more in the mind of the ecologist than geographical. We can certainly observe that there are many boundaries in nature—some fairly sharp—and what we are observing are physical manifestations between volumes wherein different conditions prevail. These are **biocycles**, subdivisions of the biosphere. Consider a lake shore, or even the water surface for that matter; the transitions between the biocycles—land, the air or atmosphere, and the body of water—are sharp and recognizable upon casual inspection. But are they really?

There is no doubt that under gravity, water in the liquid phase sorts itself out from gaseous air—a lake surface exists. But along the shore, the water moves into the earth wherever the soil or voids in the rock allow. Constantly water-saturated soil becomes a wetland. Further, atmospheric gases dissolve in the water of the lake, and molecules of water move off the lake as gaseous moisture, evident perhaps as fog on a cool morning. The sharpness of the boundaries is both actual and illusionary. Actual, because conditions encountered within each of the separate spaces or volumes (air, land, water) are very different. Illusionary, because no biocycle is completely isolated from adjacent biocycles, and typically each has influence over the other.

We have, so far considered just the physical environment. Ecosystems include organisms. And we can expect that most, though certainly not all, organisms will sort themselves out along the same physical boundaries described. That is, fish will find life conditions suitable only in the lake; conifers only in the uplands. Yet organisms are no more isolated from adjacent biocycles than are the substances of the physical world. The food of many fish will be insects living only on the land and moving through the atmosphere, which upon death or by accident, fall into the water. The conifers draw up moisture from the earth, some directly from the lake or the groundwater body connected to the lake. Ecologists use the term **biotope** to mean a topographic unit characterized by a particular set of physical conditions and a uniform assemblage of plant and animal species. Considering our example above, the lake is part of the major freshwater *biocycle* and would be a *biotope* of the region in which it is located, being perhaps just one of many ponds and lakes comprising that biotope. A **biochore** is a subdivision of the biosphere consisting of the biotopes that resemble one another; thus, our lake is but one example of the temperate zone, freshwater, lake *biochore*.

The terms "biotope", "biochore", and "biocycle" fill a need in descriptive ecology. We can speak in a general way about the life forms and climatic conditions that constitute a desert biochore, or a northern forest biochore. And we can describe, from our example illustrated by the photograph, lake, marsh, and upland forest biotopes, each with a distinct listing of species perhaps unique to just that geographical region near Minsk (in our photo example), or more broadly represented across the continent.

Gaia Theory

Consider the importance of the functional relationships between species comprising an ecosystem, and how those relationships contribute to the very survival of the ecosystem. Consider that ecosystems are not, in most cases, isolated units, but parts of a larger functioning whole, at its broadest being the biosphere. Is it possible that biosphere—all life on earth and at least those physical things utilized and modified by life on earth—is one, large integrated system?

- Read Gaia Theory (Follow links that interest you.)

Species and Habitat

In biology, the concept of **species** is basic. A species comprises a group of related organisms that share a more or less distinctive form and are capable of interbreeding. According to Ernst Mayr, species are:

> *groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups.*

- Read Species (Although you will be familiar with this material from biology studies, you should explore the topic to satisfy a more complete understanding)

In biology, it is generally the case that focus on the species concept is largely the concern of taxonomy and taxonomists. In ecology, the more important aspect is that of the **species population** (or **population** as we shall more often use the term). Note in Mayr's simple definition, that "interbreeding populations" is somewhat central. In ecology we are less concerned with all considerations of what "potentially interbreeding" might mean and more interested in the group of individuals that are, in fact, interbreeding. By which is meant, not that sexual reproduction must take place between all extant (living at the same time) members, but that there exists a gene pool that is open and potentially contributed to by each member. The concept of species would admit all those individuals separated by great distances and physical barriers as included if breeding could still take place. The species population takes into account the isolation that might actually exist, frequently dividing a single species into more than one population. Within the population, alleles presumably flow freely through time, held (at any given point in time) within the nuclei of the cells of the individual organisms constituting the population.

Using the term habitat in describing the ecological conditions surrounding an assemblage of species or a community, we are speaking of a *biotope*. Many ecologists extend the term habitat in the manner originally defined to cover physical parameters relative to a community of species, but others would substitute the term "biotope" for "habitat" in such cases. Note that this is not exactly the same as "biotope" defined above, which included the biota as well as the physical or abiotic environment. Odum (1959, p. 28) stated that "habitat... includes other organisms as well as the abiotic environment... [but a] description of the habitat of the community would include only the latter"—a point of view opposite to that expressed by most ecologists today.

Any term in ecology that attempts to separate the biotic and abiotic components of an ecological unit of organisation will encounter this difficulty. Consider that if the habitat of a bird is the place it lives, and the bird lives in a pine forest (actually up among the branches of the pine trees), then the physical environment (the "habitat") of that bird species must include a life form (pine trees); and now extend this reasoning to any manner of invertebrates, such as flea or tapeworm, that really do live most of their life on or in other organisms. A reasonably solid definition of *habitat* would be simply **the environment of a species** (Sweet, 2005).

- Read Habitat (You need follow links only as necessary to clarify terms; include the following:)
  - Read Biotope

A **niche** or *ecological niche* is essentially what a species does. We do not mean so much what activities it participates in (although these could be pertinent), but the role the species plays in the functioning of the ecosystem: the "functional status of an organism in its community" (Charles Elton, in Odum, 1959).

- Read Niche (You need follow links only as necessary to clarify terms)

Habitat Selection

The choice of habitat affects reproductive success. How do species choose which place to inhabit? Wecker (1963) and Klopfer (1963) determined this choice is partly genetic. It is also partly psychological. Habitat selection is a common behavior among vertebrates. Garter snakes (*Thamnophis elegans*) choose rocks of intermediate thickness over thicker or thinner rocks, maintaining their preferred body temperature for extended periods (Huey et al. 1989, Huey 1991). Many species show some flexibility in habitat selection. Organisms are often forced to make these choices, sometimes choosing less suitable habitats. Optimal habitats are occupied more quickly, then marginal habitats, then poor habitats, where reproductive success is limited (Fretwell and Lucas 1969).

We have just touched upon the many aspects of the biology of species populations that concern or interest us as ecologists and this topic will be much expanded upon in Chapter 5 of the *Guide*.

Summarization

There is but one known **biosphere**, that of the planet earth. The biosphere can be subdivided into a number of **biocycles**, each with fairly specific gross physical characteristics and limited by geography and topography as determined by planetary dynamics, especially gravity. Biocycles are divided into **biochores**, units with both similar basic physical attributes and life forms. Biochores are made up of a multitude of **biotopes**, divisions of the landscape that feature both similar physical attributes and a more or less consistent species composition. Some ecologists would use "biotope" for just the physical properties of this level of organisation, and **biocoenosis** for the biotic component. However, such definitional division of highly integrated and complex ecological systems is difficult to uphold. At the level of the species **population** (essentially an organism and its relatives), the habitat describes where it is found, where that species occurs in the landscape. The very different term, **niche**, describes what that organism does as a functional role in the ecosystem. The ecosystem concept differs from traditional (or the "old") biology by its clear emphasis on functional relationships among organisms.

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1.6: KEY TERMS

abstract
opening section of a scientific paper that summarizes the research and conclusions

applied science
form of science that aims to solve real-world problems

atom
smallest and most fundamental unit of matter that retains the properties of an element

basic science
science that seeks to expand knowledge and understanding regardless of the short-term application of that knowledge

biochemistry
study of the chemistry of biological organisms

biology
the study of life

biosphere
collection of all the ecosystems on Earth

botany
study of plants

cell
smallest fundamental unit of structure and function in living things

community
set of populations inhabiting a particular area

conclusion
section of a scientific paper that summarizes the importance of the experimental findings

control
part of an experiment that does not change during the experiment

deductive reasoning
form of logical thinking that uses a general inclusive statement to predict specific results

descriptive science
(also, discovery science) form of science that aims to observe, explore, and investigate

discussion
section of a scientific paper in which the author interprets experimental results, describes how variables may be related, and attempts to explain the phenomenon in question

ecosystem
all the living things in a particular area together with the abiotic, nonliving parts of that environment

eukaryote
organism with cells that have nuclei and membrane-bound organelles

evolution
the process of gradual change in a population or species over time

falsifiable
able to be disproven by experimental results

homeostasis
ability of an organism to maintain constant internal conditions

hypothesis
suggested explanation for an observation, which one can test

hypothesis-based science
form of science that begins with a specific question and potential testable answers

inductive reasoning
form of logical thinking that uses related observations to arrive at a general conclusion

introduction
opening section of a scientific paper, which provides background information about what was known in the field prior to the research reported in the paper

life science
field of science, such as biology, that studies living things

macromolecule
large molecule, typically formed by the joining of smaller molecules

materials and methods
section of a scientific paper that includes a complete description of the substances, methods, and techniques that the researchers used to gather data

microbiology
study of the structure and function of microorganisms

molecular biology
study of biological processes and their regulation at the molecular level, including interactions among molecules such as DNA, RNA, and proteins

molecule
chemical structure consisting of at least two atoms held together by one or more chemical bonds

natural science
field of science that is related to the physical world and its phenomena and processes

neurobiology
study of the biology of the nervous system

organ
collection of related tissues grouped together performing a common function

organ system
level of organization that consists of functionally related interacting organs

organelle
small structures that exist within cells and carry out cellular functions

organism
individual living entity

paleontology

study of life’s history by means of fossils

peer-reviewed manuscript
scientific paper that a scientist’s colleagues review who are experts in the field of study

phylogenetic tree
diagram showing the evolutionary relationships among various biological species based on similarities and differences in genetic or physical traits or both; in essence, a hypothesis concerning evolutionary connections

physical science
field of science, such as geology, astronomy, physics, and chemistry, that studies nonliving matter

plagiarism
using other people’s work or ideas without proper citation, creating the false impression that those are the author’s original ideas

population
all of the individuals of a species living within a specific area

prokaryote
single-celled organism that lacks organelles and does not have nuclei surrounded by a nuclear membrane

results
section of a scientific paper in which the author narrates the experimental findings and presents relevant figures, pictures, diagrams, graphs, and tables, without any further interpretation

review article
paper that summarizes and comments on findings that were published as primary literature

science
knowledge that covers general truths or the operation of general laws, especially when acquired and tested by the scientific method

scientific method
method of research with defined steps that include observation, formulation of a hypothesis, testing, and confirming or falsifying the hypothesis

serendipity
fortunate accident or a lucky surprise

theory
tested and confirmed explanation for observations or phenomena

tissue
group of similar cells carrying out related functions

variable
part of an experiment that the experimenter can vary or change

zoology
study of animals

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1.7: CHAPTER SUMMARY

1.1 THE SCIENCE OF BIOLOGY

Biology is the science that studies living organisms and their interactions with one another and their environments. Science attempts to describe and understand the nature of the universe in whole or in part by rational means. Science has many fields. Those fields related to the physical world and its phenomena are natural sciences.

Science can be basic or applied. The main goal of basic science is to expand knowledge without any expectation of short-term practical application of that knowledge. The primary goal of applied research, however, is to solve practical problems.

Science uses two types of logical reasoning. Inductive reasoning uses particular results to produce general scientific principles. Deductive reasoning is a form of logical thinking that predicts results by applying general principles. The common thread throughout scientific research is using the scientific method, a step-based process that consists of making observations, defining a problem, posing hypotheses, testing these hypotheses, and drawing one or more conclusions. The testing uses proper controls. Scientists present their results in peer-reviewed scientific papers published in scientific journals. A scientific research paper consists of several well-defined sections: introduction, materials and methods, results, and, finally, a concluding discussion. Review papers summarize the conducted research in a particular field over a period of time.

1.2 THEMES AND CONCEPTS OF BIOLOGY

Biology is the science of life. All living organisms share several key properties such as order, sensitivity or response to stimuli, reproduction, growth and development, regulation, homeostasis, and energy processing. Living things are highly organized parts of a hierarchy that includes atoms, molecules, organelles, cells, tissues, organs, and organ systems. In turn, biologists group organisms as populations, communities, ecosystems, and the biosphere. The great diversity of life today evolved from less-diverse ancestral organisms over billions of years. We can use a phylogenetic tree to show evolutionary relationships among organisms.

Biology is very broad and includes many branches and subdisciplines. Examples include molecular biology, microbiology, neurobiology, zoology, and botany, among others.

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1.8: VISUAL CONNECTION QUESTIONS

1.

Figure 1.6 In the example below, the scientific method is used to solve an everyday problem. Match 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	a. There is something wrong with the electrical outlet.
2. Question	b. If something is wrong with the outlet, my coffeemaker also won't work when plugged into it.
3. Hypothesis (answer)	c. My toaster doesn't toast my bread.
4. Prediction	d. I plug my coffee maker into the outlet.
5. Experiment	e. My coffeemaker works.
6. Result	f. Why doesn't my toaster work?

2.

Figure 1.7 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, each daughter cell will have the same chromosome set as the mother cell.
4. Animals as diverse as humans, insects, and wolves all exhibit social behavior. Therefore, social behavior must have an evolutionary advantage.

3.

Figure 1.16 Which of the following statements is false?

1. Tissues exist within organs which exist within organ systems.
2. Communities exist within populations which exist within ecosystems.
3. Organelles exist within cells which exist within tissues.
4. Communities exist within ecosystems which exist in the biosphere.

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1.9: REVIEW QUESTIONS

4.

The first forms of life on Earth were _____.

1. plants
2. microorganisms
3. birds
4. dinosaurs

5.

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

1. hypothesis
2. variable
3. theory
4. control

6.

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

1. biology
2. astronomy
3. physics
4. computer science

7.

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

1. deductive reasoning
2. the scientific method
3. hypothesis-based science
4. inductive reasoning

8.

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

1. publication
2. public speaking
3. peer review
4. the scientific method

9.

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?

1. inductive reasoning
2. deductive reasoning
3. neither, because no hypothesis was made
4. both inductive and deductive reasoning

10.

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

1. organ
2. organelle
3. cell
4. macromolecule

11.

Viruses are not considered living because they _____.

1. are not made of cells

2. lack cell nuclei
3. do not contain DNA or RNA
4. cannot reproduce

12.

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

1. prokaryotic cells
2. eukaryotic cells
3. living organisms
4. bacteria

13.

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

1. family
2. community
3. population
4. ecosystem

14.

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

1. organelle, tissue, biosphere, ecosystem, population
2. organ, organism, tissue, organelle, molecule
3. organism, community, biosphere, molecule, tissue, organ
4. biosphere, ecosystem, community, population, organism

15.

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

1. at the base
2. within the branches
3. at the nodes
4. at the branch tips

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1.10: CRITICAL THINKING QUESTIONS

16.

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.

17.

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

18.

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.

19.

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.

20.

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

21.

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.

22.

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

23.

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

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CHAPTER OVERVIEW

2: ECOLOGY AND THE BIOSPHERE

Humans are a part of the ecological landscape, and human health is one important part of human interaction with our physical and living environment.

2.1: Introduction
2.2: The Scope of Ecology
2.3: The Abiotic World
2.4: Biogeography
2.5: Terrestrial Biomes
2.6: Aquatic Biomes
2.7: Climate and the Effects of Global Climate Change
2.8: Key Terms
2.9: Chapter Summary
2.10: Visual Connection Questions
2.11: Review Questions
2.12: Critical Thinking Questions

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2.1: INTRODUCTION

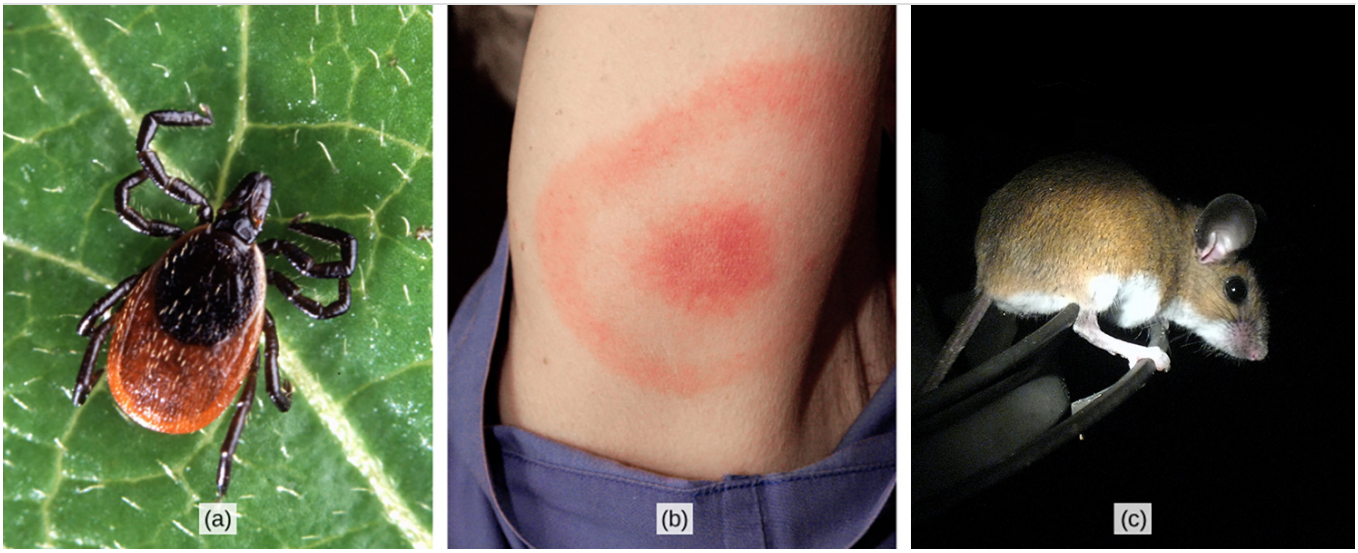


Figure 44.1 The (a) deer tick carries the bacterium that produces Lyme disease in humans, often evident in (b) a symptomatic bull's eye rash. The (c) white-footed mouse is one well-known host to deer ticks carrying the Lyme disease bacterium. (credit a: modification of work by Scott Bauer, USDA ARS; credit b: modification of work by James Gathany, CDC; credit c: modification of work by Rob Ireton)

CHAPTER OUTLINE

44.1 The Scope of Ecology
44.2 Biogeography
44.3 Terrestrial Biomes
44.4 Aquatic Biomes
44.5 Climate and the Effects of Global Climate Change

Why study ecology? Perhaps you are interested in learning about the natural world and how living things have adapted to the physical conditions of their environment. Or, perhaps you're a future physician seeking to understand the connection between your patients' health and their environment.

Humans are a part of the ecological landscape, and human health is one important part of human interaction with our physical and living environment. Lyme disease, for instance, serves as one modern-day example of the connection between our health and the natural world (Figure 44.1). More formally known as Lyme borreliosis, Lyme disease is a bacterial infection that can be transmitted to humans when they are bitten by the deer tick (*Ixodes scapularis* in the eastern U.S., and *Ixodes pacificus* along the Pacific coast). Deer ticks are the primary *vectors* (a vector is an organism that transmits a pathogen) for this disease. However, not all ticks carry the pathogen, and not all deer ticks carry the bacteria that will cause Lyme disease in humans. Also, the ticks *I. scapularis* and *pacificus* can have other hosts besides deer. In fact, it turns out that the *probability of infection* depends on the type of host upon which the tick develops: a higher proportion of ticks that live on white-footed mice carry the bacterium than do ticks that live on deer. Knowledge about the environments and population densities in which the host species is abundant would help a physician or an epidemiologist better understand how Lyme disease is transmitted and how its incidence could be reduced.

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2.2: THE SCOPE OF ECOLOGY

LEARNING OBJECTIVES

By the end of this section, you will be able to do the following:

- Define ecology and the four basic levels of ecological research
- Describe examples of the ways in which ecology requires the integration of different scientific disciplines
- Distinguish between abiotic and biotic components of the environment
- Recognize the relationship between abiotic and biotic components of the environment

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 mathematics, statistics, biochemistry, molecular biology, physiology, evolution, biodiversity, geology, and climatology.

LINK TO LEARNING

LINK TO LEARNING

Climate change can alter where organisms live, which can sometimes directly affect human health. Watch the PBS video "Feeling the Effects of Climate Change" in which researchers discover a pathogenic organism living far outside of its normal range.

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 general levels, which sometimes overlap. These levels are organism, population, community, and ecosystem (Figure 44.2).

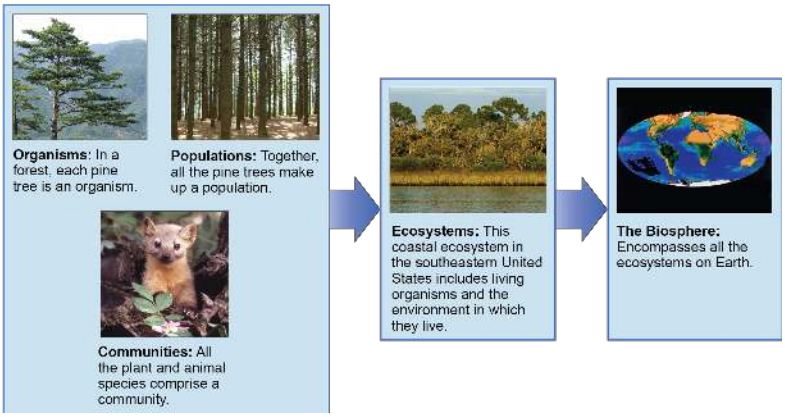


Figure 44.2 Ecologists study within several biological levels of organization. (credit "organisms": modification of work by yeowatzup"/Flickr; credit "populations": modification of work by "Crystl"/Flickr; credit "communities": modification of work by US Fish and Wildlife Service; credit "ecosystems": 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 44.3) is considered a specialist because the females only *oviposit* (that is, lay eggs) on wild lupine (*Lupinus perennis*). This specific

requirement and adaptation means that the Karner blue butterfly is completely dependent on the presence of wild lupine plants for its survival.



Figure 44.3 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 (first instar) caterpillars emerge and spend four to six weeks feeding solely on wild lupine (Figure 44.4). The caterpillars pupate as a chrysalis to undergo the final stage of 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, such as milkweeds. Generally there are two broods of the Karner blue each year.

A researcher interested in studying Karner blue butterflies at the organismal level might, in addition to asking questions about egg laying requirements, ask questions about the butterflies' preferred thoracic flight temperature (a physiological question), or the behavior of the caterpillars when they are at different larval stages (a behavioral question).



Figure 44.4 The wild lupine (*Lupinus perennis*) is the only known host plant for the Karner blue butterfly.

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 artificial boundaries may be 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.

For example, population ecologists are particularly interested in counting the Karner blue butterfly because it is classified as a federally endangered species. However, the distribution and density of this species is highly influenced by the distribution and abundance of wild lupine, and the biophysical environment around it. 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 between 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 (especially *Formica* spp). Mutualism is a form of 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 survival when ants protect Karner blue butterfly larvae (caterpillars) from predaceous insects and spiders, an act known as "tending." 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, to attract the ants, the Karner blue butterfly larvae secrete ant-like pheromones and 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, although the species of attendant ants may be partially opportunistic and vary over the range of the butterfly.

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 (nonliving 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 through 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, though the biotic and abiotic portions of the ecosystem.

CAREER CONNECTION

CAREER CONNECTION

EcologistA 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 44.5). 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 at least 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 solid foundation in mathematics and statistics.



Figure 44.5 This landscape ecologist is releasing a black-footed ferret into its native habitat as part of a study. (credit: USFWS Mountain Prairie Region, NPS)

LINK TO LEARNING

LINK TO LEARNING

Visit this site to see Stephen Wing, a marine ecologist from the University of Otago, discuss the role of an ecologist and the types of issues ecologists explore.

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SECTION OVERVIEW

2.3: The Abiotic World

The most basic interest of ecologists is how organisms interact with their environment. Inanimate objects do not normally "interact"—they are simply acted upon by forces in the environment. Organisms, however, cannot be totally passive within a chain of events and still sustain life. In a sense, life represents a reversal of the "normal" order of things in a universe where physical and chemical reactions proceed, on balance—and usually rather directly—towards lower energy states.



When a volcano erupts it lays down rocks on the surface of its slopes. These rocks are elevated in energy state from their previous existence as physical material deep within the earth. But on balance, in order to erupt, that material was first heated until fluid, and then tremendous amounts of energy expended (as pressure) to push the material (magma) up to spew as lava from the top of the mountain. Only a small portion of that energy remains on the volcano in the form of potential energy of rocks perched on the surface. That potential energy will eventually be released after forces of erosion loosen the rocks and they roll downslope or are ground to silt and deposited in the ocean deep.

In essence, the physical environment (as distinct from the biological environment) is composed of various forms of matter and energy. The physical environment is one of material acted upon by various forces (energy), resulting in a lower energy state of the material with a concomitant release or conversion of energy as (usually) heat or light.

- Read Laws of Thermodynamics (Links need not be pursued at this time)
- Read Chapter on entropy in the Wikibook, *Systems Theory*
- Read Entropy (You need not delve into the mathematics unless so inclined; this article goes beyond "Basic Ecology" requirements)
- Read Time's arrow (This article will give you insight on why the concept of entropy even matters; remember, ecology is concerned with events at the macroscopic level)

Living systems—organisms—respond in various ways to contacts with the physical forces of an ever-changing environment and interrelationships with other living organisms. The hereditary potentialities of an organism determine what it *can* do, but the environment determines what it actually *does* and to what degree (Greulach & Adams, 1962). This theme is important and you will see it repeated in the discussions that follow.

Organism responses can be described under four different categories:

- morphological,
- physiological,
- behavioural, and
- community relations.

Although these are more or less distinct categories and will be discussed in detail in this chapter, an organism's response to an environmental challenge seldom involves just one of these. At the very least, the growth or development of a morphological feature

involves internal physiological processes occurring between the genetic blue-print in the cells and some final expression of an anatomical trait. A protective morphological trait like horns on a bull come into play through behavioral actions. The horns are not a threat to a predator until wielded in an effective manner.

The Physical Environment

Why are all species not evenly distributed over the earth? A number of *abiotic* (non-living) factors shape the ecological patterns we observe over the face of the earth. Those factors include: water, temperature, wind, salt concentration, pH and the fact that the world is round. The fact that the earth is round has a substantial impact on the distribution of solar radiation, precipitation and wind across the Earth's surface. It is also responsible for the major movements of oceans. All of these abiotic factors naturally play an important role in the distribution and abundance of organisms across the globe.

Solar irradiation affects temperatures on Earth. Most organisms are **mesophiles** that like temperatures between 20-40 degrees C, some organisms are **psychrophiles** that like temperatures below 20 degrees C (cold-living organisms), and some organisms are **thermophiles** that like temperatures above 40 degrees C (heat-living organisms). Seasonality is somewhat associated with temperature. Some of the effects of seasonality include- (1) hibernation due to temperature and scarce resources, (2) rainfall/precipitation that determines how well certain plants or trees grow, and (3) wind.

Another aspect that is important to the diversity of animals' location is the amount of oxygen that is present in the particular area. For example, some organisms are **aerobes** which need oxygen for survival, and some are **anaerobes** which require the absence of oxygen for survival . However, not all organisms require the same amount of oxygen. Some organisms are **microaerophiles** and require little oxygen in order to live, but those organisms still do require oxygen for survival although it may not be as much as other organisms.

Dissolved oxygen plays a major role in supporting life in bodies of water. The greater the amount of oxygen in a body of water the more organisms the water can support. Algae release oxygen into the water which is later consumed by organisms during respiration. This process is efficient in the summer when the algae can consume adequate amount of sunlight. When lakes freeze over in the winter the snow covered ice blocks the sunlight from the algae. This causes a drop in oxygen production in the body of water since the organisms continue to respire. Low dissolved oxygen can cause a problem with predator/prey interactions within an ecosystem. Different organisms have different tolerance to low oxygen. If the predator can survive more efficiently than the prey, the amount of prey will rapidly decline. This can have a major effect on an entire food web. An experiment of this was conducted in the Chesapeake Bay. [[1]]

Water also plays a major role in the diversification of organisms throughout the world. As previously mentioned, the amount of precipitation is vital for plants to grow, which can provide food (serve as a food source) to other organisms. The salt concentration (salinity) is an important aspect to look at when dealing with water because some organisms are **halophiles** which are organisms that require salt in order to survive. The currents of the water that makes up the oceans is also important. The **gyres** are the surface currents in the oceans. The gyres distribute heat from the equators towards the poles causing the polar waters to have less energy than the water at the equator. The other type of current is the deep water current that sinks to the sea floor and flows towards the equator causing the polar waters to have a higher salinity and a higher density.

Meteorology plays an important aspect to life on Earth as well. The Earth is divided into three main parts- (1) Hadley Cell which is characterized as having Northeast trade winds and is mostly desert landscaping because of the cool, dry air, (2) Ferrell Cell which is characterized as having Westerlie winds, and (3) Polar Cell which is at the North and South poles of the Earth. The weather and wind effects plant dispersal (pollen and seeds getting blown) and the weather and the wind also effect the habitat range from which organisms can live in.

The pH is also a factor that contributes to life. The pH of the **ocean** is approximately 8.2. A deviation from this pH is slowly occurring, known as **ocean acidification**. Over a period of 243 years the pH of the ocean has dropped 0.075 in its pH. This slow acidification is a primary concern for calcium carbonate organisms. Structures made of calcium, including skeletons, are vulnerable to dissolution at lower pHs. **Soil** pH can range from 4.5 to 8.0, depending on area and vegetation growth. The main macronutrients in soil for vegetation are calcium, phosphorus, nitrogen, potassium, magnesium,and sulfur. Most vegetation prefers neutral to slightly basic or alkaline pH level, because at this level the macronutrients are readily picked up. **Rain water** is slightly acidic, depending on the amount of carbonic acid present. The average pH for rain water is 5.7. **Natural freshwaters**, such as lakes and

streams, are also slightly acidic with a pH from 5.5 to 7.7. Drastic alteration in pH levels can have devastating effects. One example is **acid rain**. Acid rain has been known to destroy everything it touches, from minerals, to plant life, to animal and human life. To learn more about acid rain visit [[2]].

- Read Ocean Acidification

The effect of wind on biodiversity varies greatly from one region to the next. For example, in southeast Alaskan rainforests, wind shapes the forests and the extent at which forests are composed. [[3]] While in other parts of the world wind driven damage from hurricanes and tornadoes affect the biodiversity by destroying trees and plants used for food and shelter. Storms are partially driven by wind currents, which in turn bring more moisture to certain areas of the planet. Wind also has a major effect on the amount of time it takes water to evaporate back into the atmosphere. A pond will hold water longer when no wind is present to intensify the drying effect. Wildfires that destroy habitat for plants and animals can be greatly manipulated by winds. Winds can spread fires quickly and over great distances to further disrupt biodiversity.

Another major effect of wind is erosion. Deserts are continuously being moved and reshaped by erosion and sandstorms caused by wind displacing sand from one terrirory to another. Wind erosion also displaces soil for plant growth by removing the most fertile top layer of soil from the earth. Soil erosion limits the growth of plants and the diversity of animals and insects that feed on these plants.



The Dust Bowl in the 1930s is an excellent example of wind destruction across the plains of North America.

The dispersal of plants is greatly effected by wind driven pollen and seed distribution. Birds that feed on small wind driven seeds from one area will excrete the seeds in another area and in turn the seed can end up in numerous areas after being blown to one or two areas. The distribution of pollen and the cross pollination on plants brings more opportunities for animals to feed and have shelter, increasing the chance for reproduction and biodiversity. With deforestation diversity is greatly reduced, but winds without the obstruction of trees allow seeds and spores to be spread over a greater distance. This will help regenerate lost habitat and increase biodiversity. [[4]]

The fact that the Earth is round leads to several of the aspects that have been previously mentioned in the above paragraphs. Since the Earth is round, solar irradiation is distributed unevenly across the Earth's surface, which simply means that more solar radiation hits at the equator than at the poles. The less solar irradiation you have, the less energy there is, causing less biomass (living organisms and less diversity). All forms of life require some quantity of solar radiation in order to survive, but the amount varies from organism to organism.

Why does the temperature vary so greatly from the tropics to the poles? It is not simply a matter of more incident irradiation hitting the equator. Rather more irradiation impinges on a smaller area near the equator when compared to the poles. Furthermore, because sunlight strikes the poles at an angle it must traverse more of the atmosphere before being absorbed by the earth. As a result of having to travel through more of the atmosphere more of the solar energy is deflected or reradiated back into space. How does this impact life on earth? Less solar irradiation per unit area means that temperatures are generally cooler towards the poles which limits the kinds of organisms that may inhabit these environments. More irradiation near the equator means more energy is added to the ecosystem which translates in more *biomass*.



New problems in global ecology include rising levels of atmospheric CO_2 concentrations and other greenhouse gases, and the resultant potential changes in global climate patterns. General Circulation Models (GCMs) (see Global Climate Model) are complex computer models developed by atmospheric scientists to help predict how increasing greenhouse gas concentrations might influence global climate patterns on a large scale.

For example, elevated temperatures, which are in part due to raised concentrations of carbon dioxide, affect turtle hatchlings. The map turtle and red-eared slider turtle both have temperature-dependent sex determination. A higher temperature results in a female hatchling, whereas a lower temperature results in a male. Thus, raised temperature result in fewer male turtles.

Global warming has a great impact on biodiversity distribution and abundance. Processes and patterns of the climate influence behavioral and physiological response of organisms, their productivity, relative competitive abilities of species, birth, growth, and death rates, nutrient cycling, decomposition, net primary production, and community structure of populations.

Organism Morphology

The form that an organism takes—termed its **life-form**—encompasses all of the structural aspects that make that species describable and unique. By **morphological adaptations** is meant the structural feature or features (called traits) that allow an organism to live successfully in its habitat; traits that have evolved over a (usually long) period of time as a consequence of the process of **natural selection**.

Natural Selection is a process that occurs over several generations. It allows select organisms to adapt to their environment over time. Natural selection often results in a species being able to survive in areas with environmental restrictions. For example, a plant that can grow taller than the others around it can get more sun light then the other plants around it and will increase its chance of survival and its overall **fitness.** For Natural Selection to occur, two requirements must be met. First there must be variation in some trait and second the trait must affect either survival or reproduction or both. Natural selection can result in **Directional Selection** or **Disruptive selection**. Directional Selection is when individuals at one end of the distribution do well and the other doesn't. Disruptive selection is when there is an intermediate that does not do as well as the individuals on the other sides of the distribution.

- Read Wikipedia:en:Directional selection (for further information)
- Read Wikipedia:en:Disruptive selection
- Read Wikipedia:en:Stabilizing selection
- Read natural selection (Links need not be pursued at this time)

Although we might conclude that adaptive morphological traits are acquired by a species slowly through the evolutionary process and therefore not subject to change within the lifespan of an individual, in fact many morphological traits are expressed or modified in response to environmental conditions. The individual organism inherits morphological variation within a range, and the expression of the trait represents a response to specifics of that individual's environment. The considerable similarity of all individuals of a species attests to the genetic basis of morphological traits, yet a degree of plasticity is usually present to be influenced by environmental factors. Individuals inherit this plasticity and not the **growth-form** of the parents. Thus *growth-form*

represents the outcome of both "nature" (genetic or inherited traits) and "nurture" (influences of environment on the growth process).

A growth-form that persists through many generations because of environmental constancy (but is not an inherited trait) is termed an **ecad**. However, any such trait is subject to natural selection and may, over time, become fixed in a population as an inherited **eco-type**. That is, if the trait is highly adaptive within the habitat of the population, and the plasticity of expression is under-utilized becoming a genetic burden, that plasticity may be lost or restricted. Eco-types are genetically based differences between individuals of the same species that come from different populations.

Organism Physiology

Physiology is the study of biochemical functions of living organisms. Whereas morphology (discussed above) is essentially about anatomy and structure, physiology is largely about processes. However, the two are so interlinked in any organism that one cannot really be discussed without consideration of the other. As already noted, physiological processes must proceed the growth of morphological traits. And a physiological response, such as an increase in blood pressure, results from short-term mechanical changes in the anatomy of the heart and arteries. Put another way, the shape and structure of a heart is a morphological trait; the pumping of blood—the function of the heart organ—is a physiological activity. Muscle contractions are mechanical actions resulting from biochemical signals and changes. One cannot occur without the other.

Biologists refer to **physiological adjustment** as a response to environmental change. By "adjustment" is meant a change in physiology or internal function that allows the organism to maintain life. An adjustment is limited by the physiological and morphological adaptations inherited by the organism. Just as we previously described "morphological variation" as essentially an adjustment to environment based upon inheritance of a range of possibility, so too is physiology controlled by both inherited (genetic) and environmental (external) factors. The important distinction here is between the terms "adjustment" and "adaptation", a distinction that can apply to both morphology and physiology.

- **Adaptations** are physiological processes or morphological traits inherited through genetics and subject to natural selection at the population level;
- **Adjustments** are activities and traits expressed within an inherited range and subject to individual modification within the life-span of the individual or even much shorter periods of time. The proper term here is **acclimatization**.

If I work out and buff my body to rival that of the current Governor of California, I am not adapting but adjusting or acclimatizing myself (considerably, comparing our growth-forms!). On the other hand, when a caterpillar changes into a pupa and then transforms itself into a butterfly, that is clearly an adaptation. The process (called metamorphosis) is an inherited one, and irreversible. Aging is a process that would appear to be largely irreversible (certainly death is), and apparently is an adaptation. Once reproductive success peaks and starts to decline, advantage for the species population goes towards eliminating older individuals (fortunately, some exceptions exist).

Organism Behavior

Behavioral responses to environmental factors can be observed as movements of one sort or another. We say that "behavior" is the way an organism "acts"—what activities it "does". Complex behaviors controlled by cognitive processes evolved from simple response behaviors, the understanding of which provides a basis for understanding how behavior confers survivability on an organism. Note that such responses are generally rapid (and mediated through nerves in higher animals) in organisms capable of locomotor activity, and generally much slower in organisms lacking means of motility. Thus, plants, although devoid of musculature, nonetheless respond to **stimuli** of various sorts—growing or turning towards a light, for example. Simple turning responses, either towards or away from a specific stimulus, are termed **tropisms**. Actual physical movement towards or away from a stimulus are called **taxes**. Similar behaviours called **kineses** involve physical movements that appear random in orientation or direction, but the intensity of activity is determined by the intensity of the stimulus.

- Read Tropism (Follow links to the various examples of tropisms to understand this concept)
- Read Taxes (Follow links as necessary to understand concepts; Kineses included here as well)

Summarization

The "home" of the biosphere is the planet earth, an accretion body orbiting a star. The physical realities of the planet, resulting from its size and location relative to that star called the "sun", determine the basic physical properties within which life developed and presently exists.

Organisms respond to changes and vagaries in the environment. Organisms, unlike non-living objects, survive because of the ability to respond. Responses take many forms, which we can categorize as morphological, physiological, or behavioral. However, most responses involve a combination of these types, and sorting of responses into specific types typically just means that one is the more obvious aspect of the response observed.

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2.4: BIOGEOGRAPHY

LEARNING OBJECTIVES

By the end of this section, you will be able to do the following:

- 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 effects 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 and high insolation (sunlight).

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 and taiga 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 in many ways 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 (*Dionaea muscipula*) 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 (*Procyon* spp) 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 44.6ab).



(a) (b)

Figure 44.6 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. Despite being tropical, Hawaii, for example, has no native land species of reptiles or amphibians, only a few native species of butterflies, and only one native terrestrial mammal, the hoary bat. Most of New Guinea, as another example, lacks placental mammals.

LINK TO LEARNING

LINK TO LEARNING

Check out this video to observe a platypus swimming in its natural habitat in New South Wales, Australia.

Like animals, 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 44.7).



Figure 44.7 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. (credit: 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 that passes through the canopy. One such adaptation is the rapid growth of spring ephemeral plants such as the spring beauty (*Claytonia virginica*) (Figure 44.8). 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 44.8 The spring beauty is an ephemeral spring plant that flowers early in the spring to avoid competing with larger forest trees for sunlight. (credit: John Beetham)

In aquatic ecosystems, the availability of light may be limited because sunlight is absorbed by water, plants, suspended particles, and resident microorganisms. Toward the bottom of a lake, pond, or ocean, there is a zone that light cannot reach (because most wavelengths except for the shortest blues are absorbed by the water column). 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. You can 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.

The availability of nutrients in aquatic systems such as oceans 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 44.9). 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.

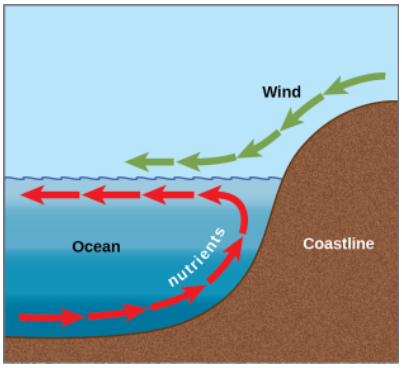


Figure 44.9 Ocean upwelling is an important process that recycles nutrients and energy in the ocean. As wind (green arrows) pushes offshore, it causes water from the ocean bottom (red arrows) to move to the surface, bringing up nutrients from the ocean depths.

In freshwater systems, such as lakes, the recycling of nutrients occurs in response to air temperature and wind changes. The nutrients at the bottom of lakes are recycled twice each year: in the spring and fall turnover. The spring-and-fall turnover are seasonal processes that recycle nutrients and oxygen from the bottom of a freshwater lake to the top of the lake (Figure 44.10). These turnovers are caused by the formation of a thermocline: layers of water with temperatures that are significantly different from those above and below it.

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 about 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 surface of the water, due to the surface ice layer.

VISUAL CONNECTION

VISUAL CONNECTION

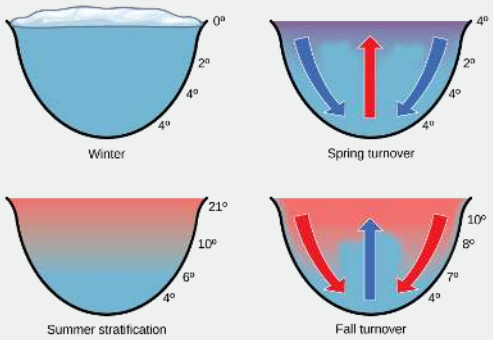


Figure 44.10 The spring and fall turnovers are important processes in freshwater lakes that act to move the nutrients and oxygen at the bottom of deep lakes to the top. Turnover occurs because water has a maximum density at 4 °C. Surface water temperature changes as the seasons progress, and denser water sinks.

How might turnover in tropical lakes differ from turnover in lakes that exist in temperate regions? Think of the variation, or lack of variation, in seasonal temperature change.

In springtime, air temperatures increase and surface ice melts. When the temperature of the surface water begins to approach 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 and denser 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. This is called the *spring turnover*. 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 44.10). During the winter, the oxygen at the bottom of the lake is

used by decomposers and other organisms requiring oxygen, such as fish. It is important to note, however, that the relative transparency of ice also allows the penetration of the shorter wavelengths of visible light so that photosynthesis, especially by algae can continue.

TEMPERATURE

Temperature affects the physiology of organisms 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 near the Earth's surface. 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 Archaea bacteria have evolved to tolerate extremely hot temperatures such as those found in the geysers within Yellowstone National Park. Such bacteria are examples of *extremophiles*: organisms that thrive in extreme environments.

The temperature (of both water and air) 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 regular 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. For example, 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 and western United States in the warmer months, where they build up enormous populations, and migrate to areas around Michoacan, Mexico as well as areas along the Pacific Coast, 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 generally lack migratory ability. Not all animals that could 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 freezing and bursting.

WATER

Water is required by all living things because it is critical for cellular processes. Since terrestrial organisms lose water to the environment, 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 and convection.
- 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 determining 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 together all 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, currents, and tidal changes 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, transpiration, and convective heat loss from the surface of all organisms. 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 (*Pinus banksiana*) requires heat from fire for its seed cones to open (Figure 44.11). Through the burning of pine needles, fire adds nitrogen to the soil and limits competition by destroying undergrowth.



Figure 44.11 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. (credit: 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 above-ground biomass per unit area, which is the total mass of living plants, excluding roots (whose mass is very difficult to measure). 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 produce 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 above-ground 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.

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2.5: TERRESTRIAL BIOMES

LEARNING OBJECTIVES

By the end of this section, you will be able to do the following:

- Identify the two major abiotic factors that determine terrestrial biomes
- Recognize distinguishing characteristics of each of the eight major 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 44.12).

VISUAL CONNECTION

VISUAL CONNECTION

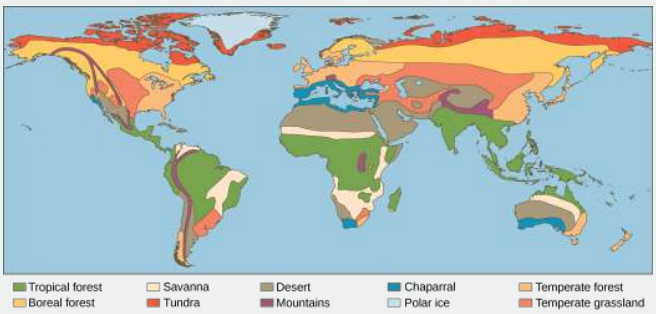


Figure 44.12 Each of the world's major biomes is distinguished by characteristic temperatures and amounts of precipitation. Polar ice and mountains are also shown.

Which of the following statements about biomes is false?

1. Chaparral is dominated by shrubs.
2. Savannas and temperate grasslands are dominated by grasses.
3. Boreal forests are dominated by deciduous trees.
4. Lichens are common in the arctic tundra.

TROPICAL WET FOREST

Tropical wet forests are also referred to as tropical rainforests. This biome is found in equatorial regions (Figure 44.12). The vegetation is characterized by plants with broad leaves that fall and are replaced 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 more temperate 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 cm 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 typically 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 44.13). 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 American Amazonian rain forest. 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 example, 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 44.13 Tropical wet forests, such as these forests along the Madre de Dios river, Peru, near the Amazon River, have high species diversity. (credit: Roosevelt Garcia)

SAVANNAS

Savannas are grasslands with scattered trees, and they are located in Africa, South America, and northern Australia (Figure 44.12). Savannas are usually 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 44.14). Since fire is an important source of disturbance in this biome, plants have evolved well-developed root systems that allow them to quickly resprout after a fire.



Figure 44.14 Savannas, like this one in Taita Hills Wildlife Sanctuary in Kenya, are dominated by grasses. (credit: 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 44.12). 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). This is largely due to the lack of atmospheric water. 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 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, and then 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 44.15). 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 44.15 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 44.12). 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 44.16, is dominated by shrubs 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 44.16 The chaparral is dominated by shrubs. (credit: 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 44.12). 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 dense enough to sustain populations of grazing animals Figure 44.17. 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 44.17 The American bison (*Bison bison*), more commonly called the buffalo, is a grazing mammal that once populated American prairies in huge numbers. (credit: 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 sometimes dense forests with drought-tolerant tree species. 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 44.12). 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 periodically during cold winters. 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 44.18). 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 44.18 Deciduous trees are the dominant plant in the temperate forest. (credit: 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 most 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, which does not develop in tropical rainforests. 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 44.12). 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 (coniferous) 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 above-ground biomass of boreal forests is high because these slow-growing tree species are long-lived and accumulate a large 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 44.19). 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 44.19 The boreal forest (taiga) has low lying plants and conifer trees. (credit: 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 44.12). The average winter temperature is –34 °C (–29.2 °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 44.20). There is little species diversity, low net primary productivity, and low above-ground 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 44.20 Low-growing plants such as shrub willow dominate the tundra landscape, shown here in the Arctic National Wildlife Refuge. (credit: USFWS Arctic National Wildlife Refuge)

LINK TO LEARNING

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.

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2.6: AQUATIC BIOMES

LEARNING OBJECTIVES

By the end of this section, you will be able to do the following:

- Describe the effects of abiotic factors on the composition of plant and animal communities in aquatic biomes
- Compare and contrast the characteristics of the ocean zones
- Summarize the characteristics of standing water and flowing water freshwater 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 and the ability to store much larger amounts of energy than the air) 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 44.21). 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.

VISUAL CONNECTION

VISUAL CONNECTION

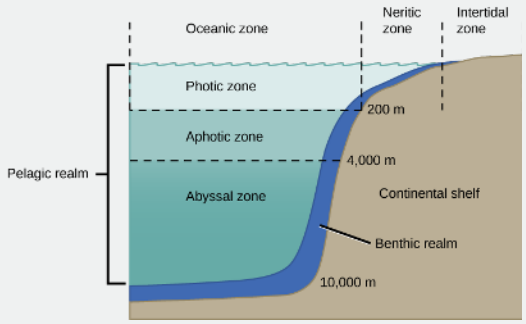


Figure 44.21 The ocean is divided into different zones based on water depth and distance from the shoreline.

In which of the following regions would you expect to find photosynthetic organisms?

1. the aphotic zone, the neritic zone, the oceanic zone, and the benthic realm
2. the photic zone, the intertidal zone, the neritic zone, and the oceanic zone
3. the photic zone, the abyssal zone, the neritic zone, and the oceanic zone
4. the pelagic realm, the aphotic zone, the neritic zone, and the oceanic zone

MARINE BIOMES

The ocean is the largest marine biome. It is a continuous body of salt water that is relatively uniform in chemical composition; in fact, 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 44.21). 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 action of tidal ebb and flow. 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 may also be repeatedly struck by waves, and the organisms found there are adapted to withstand damage from their pounding action (Figure 44.22). 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 44.22 Sea urchins, mussel shells, and starfish are often found in the intertidal zone, shown here in Kachemak Bay, Alaska. (credit: NOAA)

The neritic zone (Figure 44.21) extends from the intertidal zone to depths of about 200 m (or 650 ft) at the edge of the *continental shelf* (the underwater landmass that extends from a continent). Since light can penetrate this depth, photosynthesis can still 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 **pelagic** or **open oceanic zone** (Figure 44.21). 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, most of the open ocean lacks a process for bringing the organic nutrients back up to the surface. (Exceptions include major oceanic upwellings within the Humboldt Current along the western coast of South America.) 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 deep-water region beyond the continental shelf (Figure 44.21). The bottom of the benthic realm is composed 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 44.21) is very cold and has very high pressure, very low or no oxygen content, and high nutrient content as the dead and decomposing material that drifts down from the layers above. 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, comprising mostly cnidarians and molluscs, 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 perhaps the best-known and largest reef system in the world—visible from the International Space Station! This massive and ancient reef is 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 44.23). 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 called cnidocytes on their tentacles to capture prey.

LINK TO LEARNING

LINK TO LEARNING

Watch this National Oceanic and Atmospheric Administration (NOAA) video to see marine ecologist Dr. Peter Etnoyer discuss his research on coral organisms.

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, and planktivores, which consume planktonic organisms such as bacteria, archaea, algae, and protists floating in the pelagic zone.



Figure 44.23 Coral reefs are formed by the calcium carbonate skeletons of coral organisms, which are marine invertebrates in the phylum Cnidaria. (credit: Terry Hughes)

EVOLUTION CONNECTION

EVOLUTION CONNECTION

Global Decline of Coral Reefs It takes many thousands of years 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 lose 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 when coral animals build their calcium carbonate shelters.

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, as well, 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 can offer 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, molluscs, and fish begin their lives, which also creates important breeding grounds for other animals. Salinity is a very important factor that influences the organisms and the adaptations of the organisms found in estuaries. The salinity of estuaries varies considerably and is based on the rate of flow of its freshwater sources, which may depend on the seasonal rainfall. 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 remove oxygen from the water) to anaerobic respiration (a process that does not require oxygen and takes place in the cytoplasm of the animal's cells). 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 ecosystem benefits, which are aquatic resources for drinking water, crop irrigation, sanitation, and industry. Lakes and ponds are connected with abiotic and biotic factors influencing their 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, as we have seen, 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 larvae and adult 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 the determining factors in the amount of phytoplankton growth that takes place 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 44.24) can become so extensive that they reduce light penetration in water. They may also release toxic byproducts into the water, contaminating any drinking water taken from that source. In addition, 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, resulting in a dead zone. Lake Erie and the Gulf of Mexico represent freshwater and marine habitats where phosphorus control and storm water runoff pose significant environmental challenges.



Figure 44.24 The uncontrolled growth of algae in this lake has resulted in an algal bloom. (credit: 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 usually clear and free of debris. 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 and other organic material that fall downstream into the river or stream, as well as 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, some species of mayfly (phylum Arthropoda) have flattened bodies and legs with modified claws to help them cling to the underside of submerged rocks. This body form reduces drag and allows these species to benefit from the high oxygen concentrations in fast-moving currents without being dislodged. 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 44.25). The three shared characteristics among these types—what makes them wetlands—are their hydrology, hydrophytic vegetation, and hydric soils.



Figure 44.25 Located in southern Florida, Everglades National Park is vast array of wetland environments, including sawgrass marshes, cypress swamps, and estuarine mangrove forests. Here, a great egret walks among cypress trees. (credit: NPS)

Freshwater marshes and swamps are characterized by slow and steady water flow. Bogs, however, develop in depressions where water flow is low or nonexistent. Bogs usually occur in areas where there is a clay bottom with poor percolation of water. (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 used during the decomposition of organic matter is not readily replaced. As the oxygen in the water is depleted, decomposition slows. This leads to a buildup of acids and a lower water pH. The lower pH creates challenges for plants because it limits the available nitrogen. As a result, some bog plants (such as sundews, pitcher plants, and Venus flytraps) capture insects in order to 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.

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2.7: CLIMATE AND THE EFFECTS OF GLOBAL CLIMATE CHANGE

LEARNING OBJECTIVES

By the end of this section, you will be able to do the following:

- 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

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 gradually become increasingly evident during the last sixty years. Global climate change is the term used to describe altered global weather patterns, especially a worldwide increase in temperature and resulting changes in the climate, due largely to rising levels of atmospheric carbon dioxide.

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 Indiana) provides 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*.

Climate refers to the long-term, *predictable atmospheric conditions* of a specific area. The climate of a biome is characterized by having consistent seasonal temperature and 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. 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 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 that takes place over many years.

GLOBAL CLIMATE CHANGE

Climate change can be understood by approaching three areas of study:

- evidence of current and past global climate change
- drivers of global climate change
- It is helpful to keep these three different aspects of climate change clearly separated when consuming media reports about global climate change. We should note that 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 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 for climate change. 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 air bubbles 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 44.26a). The data represented in Figure 44.27 is an example of such analyses. 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.



Figure 44.26 Scientists drill for ice cores in polar regions. The ice contains air bubbles and biological substances that provide important information for researchers. (credit: a: Helle Astrid Kjær; b: National Ice Core Laboratory, USGS)

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 44.27b shows that the atmospheric concentration of carbon dioxide has also risen and fallen in periodic cycles. Also note the relationship between carbon dioxide concentration and temperature. Figure 44.27b shows that carbon dioxide levels in the atmosphere have historically cycled between 180 and 300 parts per million (ppm) by volume.

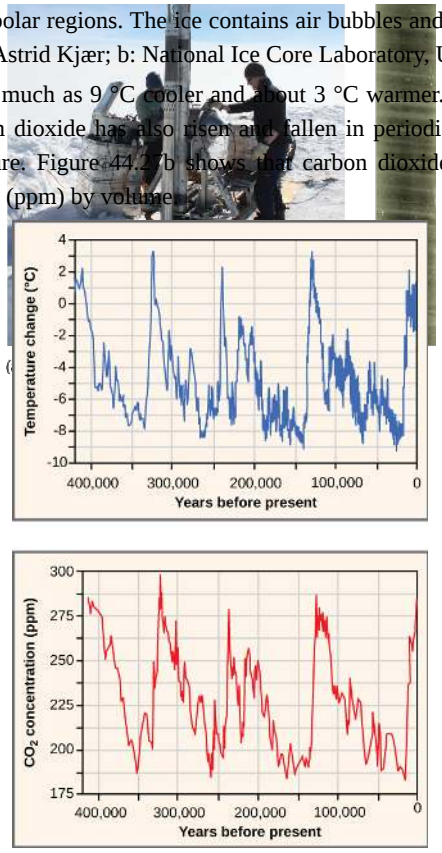


Figure 44.27 Ice at the Russian Vostok station in East Antarctica was laid down over the course of 420,000 years and reached a depth of over 3,000 m. By measuring the amount of CO_2 trapped in the ice, scientists have determined past atmospheric CO_2 concentrations. Temperatures relative to modern day were determined from the amount of *deuterium* (a nonradioactive isotope of hydrogen) present.

Figure 44.27a does not show the last 2,000 years with enough detail to compare the changes of Earth's temperature during the last 400,000 years with the temperature change that has occurred in the more recent past. Two significant temperature anomalies, or *irregularities*, have occurred in the last 2,000 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 climatic 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 the United States. New technologies were invented that 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 is burned, carbon dioxide is released. With the beginning of the Industrial Era, atmospheric carbon dioxide began to rise (Figure 44.28).

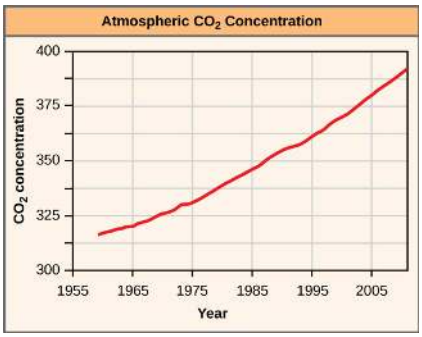


Figure 44.28 The atmospheric concentration of CO_2 has risen steadily since the beginning of industrialization.

CURRENT AND PAST DRIVERS OF GLOBAL CLIMATE CHANGE

Because it is not possible to go back in time to directly observe and measure climate, scientists must use *indirect evidence* to determine the *drivers*, or factors, 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.

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 before dissipating in intensity. In Europe and North America, haze-effect cooling produced some of the lowest average winter temperatures on record in 1783 and 1784.

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, in a similar manner as do 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 ozone. 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 (infrared) 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, heating it up and the atmosphere immediately above it. 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.

Direct 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 2011, the atmospheric carbon dioxide concentration was 392 ppm. However, the planet would not be inhabitable by current life forms if water vapor did not produce its drastic greenhouse warming effect.

Scientists look at patterns in data and try to explain differences or deviations from these patterns. 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. 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, beginning only a few centuries ago, 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? A key factor that must be recognized when comparing the historical data and the current data is the presence and industrial activities 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*.

Human activity releases carbon dioxide and methane, two of the most important greenhouse gases, into the atmosphere in several ways. The primary mechanism that releases carbon dioxide is the burning of fossil fuels, such as gasoline, coal, and natural gas (Figure 44.29). Deforestation, cement manufacture, animal agriculture, the clearing of land, and the burning of forests are other human activities that release carbon dioxide. Methane (CH_4) is produced when bacteria break down organic matter under anaerobic conditions. Anaerobic conditions can happen when organic matter is trapped underwater (such as in rice paddies) or in the intestines of herbivores. Methane can also be released from natural gas fields and the decomposition of animal and plant material that occurs in landfills. Another source of methane is the melting of *clathrates*. Clathrates are frozen chunks of ice and methane 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 of global temperatures.



Figure 44.29 The burning of fossil fuels in industry and by vehicles releases carbon dioxide and other greenhouse gases into the atmosphere. (credit: "Pöllö"/Wikimedia Commons)

DOCUMENTED RESULTS OF CLIMATE CHANGE: PAST AND PRESENT

Scientists have geological evidence of the consequences of long-ago climate change. Modern-day phenomena such as retreating glaciers and melting polar ice cause a continual rise in sea level. Meanwhile, changes in climate can negatively affect organisms.

GEOLOGICAL CLIMATE CHANGE

Global warming has 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 approximately 70 percent of the terrestrial plant and animal species and 84 percent of marine species became extinct, vanishing forever 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 (118–157 in) and 20 °C–30 °C (68 °F–86 °F) in the tropical wet forest, may not have been able to survive the Permian climate change.

LINK TO LEARNING

LINK TO LEARNING

Watch this NASA video to discover the mixed effects of global warming on plant growth. While scientists found that warmer temperatures in the 1980s and 1990s caused an increase in plant productivity, this advantage has since been counteracted by more frequent droughts.

PRESENT CLIMATE CHANGE

A number of global events have occurred that may be attributed to climate change during our lifetimes. *Glacier National Park* in Montana is undergoing the retreat of many of its glaciers, a phenomenon known as glacier recession. In 1850, the area contained approximately 150 glaciers. By 2010, however, the park contained only about 24 glaciers greater than 25 acres in size. One of these glaciers is the *Grinnell Glacier* (Figure 44.30) at Mount Gould. Between 1966 and 2005, the size of Grinnell Glacier shrank by 40

percent. Similarly, the mass of the ice sheets in Greenland and the Antarctic is decreasing: Greenland lost 150–250 km^3 of ice per year between 2002 and 2006. In addition, the size and thickness of the Arctic sea ice is decreasing.



Figure 44.30 The effect of global warming can be seen in the continuing retreat of Grinnel Glacier. The mean annual temperature in the park has increased 1.33 °C since 1900. The loss of a glacier results in the loss of summer meltwaters, sharply reducing seasonal water supplies and severely affecting local ecosystems. (credit: modification of work by USGS)

This loss of ice is leading to increases in the global sea level. 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. A variety of factors affect the volume of water in the ocean, especially the temperature of the water (the density of water is related to its temperature: water volume expands as it warms, thus raising sea levels), as well as the *amount of water* found in rivers, lakes, glaciers, polar ice caps, and sea ice. As glaciers and polar ice caps melt, there is a significant contribution of liquid water that was previously frozen.

In addition to some abiotic conditions changing in response to climate change, many organisms are also being affected by the changes in temperature. Temperature and precipitation play key roles in determining the *geographic distribution* and *phenology* of plants and animals. (Phenology is the study of the effects of climatic conditions on the timing of periodic life cycle events, such as flowering in plants or migration in birds.) Researchers have shown that 385 plant species in Great Britain are flowering 4.5 days sooner than was recorded earlier during the previous 40 years. In addition, insect-pollinated species were more likely to flower earlier than wind-pollinated species. The impact of changes in flowering date would be mitigated if the insect pollinators emerged earlier. This mismatched timing of plants and pollinators could result in injurious ecosystem effects because, for continued survival, insect-pollinated plants must flower when their pollinators are present.

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2.8: KEY TERMS

abiotic
nonliving components of the environment

above-ground biomass
total mass of aboveground living plants per area

abyssal zone
deepest part of the ocean at depths of 4000 m or greater

algal bloom
rapid increase of algae in an aquatic system

aphotic zone
part of the ocean where no light penetrates

benthic realm
(also, benthic zone) part of the ocean that extends along the ocean bottom from the shoreline to the deepest parts of the ocean floor

biogeography
study of the geographic distribution of living things and the abiotic factors that affect their distribution

biome
ecological community of plants, animals, and other organisms that is adapted to a characteristic set of environmental conditions

biotic
living components of the environment

canopy
branches and foliage of trees that form a layer of overhead coverage in a forest

channel
width of a river or stream from one bank to the other bank

clathrates
frozen chunks of ice and methane found at the bottom of the ocean

climate
long-term, predictable atmospheric conditions present in a specific area

conspecifics
individuals that are members of the same species

coral reef
ocean ridges formed by marine invertebrates living in warm, shallow waters within the photic zone

cryptofauna
invertebrates found within the calcium carbonate substrate of coral reefs

ecology
study of interaction between living things and their environment

ecosystem services
human benefits and services provided by natural ecosystems

emergent vegetation

wetland plants that are rooted in the soil but have portions of leaves, stems, and flowers extending above the water's surface

endemic
species found only in a specific geographic area that is usually restricted in size

estuary
biomes where a source of fresh water, such as a river, meets the ocean

fall and spring turnover
seasonal process that recycles nutrients and oxygen from the bottom of a freshwater ecosystem to the top

global climate change
altered global weather patterns, including a worldwide increase in temperature, due largely to rising levels of atmospheric carbon dioxide

greenhouse effect
warming of Earth due to carbon dioxide and other greenhouse gases in the atmosphere

greenhouse gases
atmospheric gases such as carbon dioxide and methane that absorb and emit radiation, thus trapping heat in Earth's atmosphere

haze-effect cooling
effect of the gases and solids from a volcanic eruption on global climate

heterospecifics
individuals that are members of different species

intertidal zone
part of the ocean that is closest to land; parts extend above the water at low tide

Milankovitch cycles
cyclic changes in the Earth's orbit that may affect climate

neritic zone
part of the ocean that extends from low tide to the edge of the continental shelf

net primary productivity
measurement of the energy accumulation within an ecosystem, calculated as the total amount of carbon fixed per year minus the amount that is oxidized during cellular respiration

ocean upwelling
rising of deep ocean waters that occurs when prevailing winds blow along surface waters near a coastline

oceanic zone
part of the ocean that begins offshore where the water measures 200 m deep or deeper

pelagic realm
(also, pelagic zone) open ocean waters that are not close to the bottom or near the shore

permafrost
perennially frozen portion of the Arctic tundra soil

photic zone
portion of the ocean that light can penetrate

planktivore
animal species that eats plankton

predator

organism that kills and consumes another organism

Sargassum

type of free-floating marine seaweed

solar intensity

amount of solar power energy the sun emits in a given amount of time

source water

point of origin of a river or stream

thermocline

layer of water with a temperature that is significantly different from that of the surrounding layers

weather

conditions of the atmosphere during a short period of time

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2.9: CHAPTER SUMMARY

44.1 THE SCOPE OF ECOLOGY

Ecology is the study of the interactions of living things with their environment. Ecologists ask questions that comprise four levels of general biological organization—organismal, population, community, and ecosystem. At the organismal level, ecologists study individual organisms and how they interact with their environments. At the population and community levels, ecologists explore, respectively, how a population of organisms changes over time and the ways in which that population interacts with other species in the community. Ecologists studying an ecosystem examine the living species (the biotic components) of the ecosystem as well as the nonliving portions (the abiotic components), such as air, water, and soil, of the environment.

44.2 BIOGEOGRAPHY

Biogeography is the study of the geographic distribution of living things as well as 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 a species is found. Ocean upwellings, 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.

44.3 TERRESTRIAL BIOMES

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 and supply energy for high diversity throughout the food web. Other biomes, such as deserts and tundras, have low primary productivity due to extreme temperatures and a shortage of available water.

44.4 AQUATIC BIOMES

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.

44.5 CLIMATE AND THE EFFECTS OF GLOBAL CLIMATE CHANGE

The Earth has gone through periodic cycles of increases and decreases in temperature. During the past 2,000 years, the Medieval Climate Anomaly was a warmer period, while the Little Ice Age was unusually cool. Both of these irregularities can be explained by natural causes of changes in climate, and, although the temperature changes were small, they had significant effects. Natural drivers of climate change include Milankovitch cycles, changes in solar activity, and volcanic eruptions. None of these factors, however, leads to rapid increases in global temperature or sustained increases in carbon dioxide.

The burning of fossil fuels is an important source of greenhouse gases, which play a major role in the greenhouse effect. Two hundred and fifty million years ago, global warming resulted in the Permian extinction: a large-scale extinction event that is documented in the fossil record. Currently, modern-day climate change is associated with the increased melting of glaciers and polar ice sheets, resulting in a gradual increase in sea level. Plants and animals can also be affected by global climate change when the timing of seasonal events, such as flowering or pollination, is affected by global warming.

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2.10: VISUAL CONNECTION QUESTIONS

1.

Figure 44.10 How might turnover in tropical lakes differ from turnover in lakes that exist in temperate regions? Think of the variation, or lack of variation, in seasonal temperature change.

2.

Figure 44.12 Which of the following statements about biomes is false?

1. Chaparral is dominated by shrubs.
2. Savannas and temperate grasslands are dominated by grasses.
3. Boreal forests are dominated by deciduous trees.
4. Lichens are common in the arctic tundra.

3.

Figure 44.21 In which of the following regions would you expect to find photosynthetic organisms?

1. the aphotic zone, the neritic zone, the oceanic zone, and the benthic realm
2. the photic zone, the intertidal zone, the neritic zone, and the oceanic zone
3. the photic zone, the abyssal zone, the neritic zone, and the oceanic zone
4. the pelagic realm, the aphotic zone, the neritic zone, and the oceanic zone

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2.11: REVIEW QUESTIONS

4.

Which of the following is a biotic factor?

1. wind
2. disease-causing microbe
3. temperature
4. soil particle size

5.

The study of nutrient cycling though the environment is an example of which of the following?

1. organismal ecology
2. population ecology
3. community ecology
4. ecosystem ecology

6.

Understory plants in a temperate forest have adaptations to capture limited _____.

1. water
2. nutrients
3. heat
4. sunlight

7.

An ecologist hiking up a mountain may notice different biomes along the way due to changes in all of the following except:

1. elevation
2. rainfall
3. latitude
4. temperature

8.

Which of the following biomes is characterized by abundant water resources?

1. deserts
2. boreal forests
3. savannas
4. tropical wet forests

9.

Which of the following biomes is characterized by short growing seasons?

1. deserts
2. tropical wet forests
3. Arctic tundras
4. savannas

10.

Where would you expect to find the most photosynthesis in an ocean biome?

1. aphotic zone
2. abyssal zone
3. benthic realm
4. intertidal zone

11.

A key feature of estuaries is:

1. low light conditions and high productivity
2. salt water and fresh water

3. frequent algal blooms
4. little or no vegetation

12.

Which of the following is an example of a weather event?

1. The hurricane season lasts from June 1 through November 30.
2. The amount of atmospheric CO_2 has steadily increased during the last century.
3. A windstorm blew down trees in the Boundary Waters Canoe Area in Minnesota on July 4, 1999.
4. Deserts are generally dry ecosystems having very little rainfall.

13.

Which of the following natural forces is responsible for the release of carbon dioxide and other atmospheric gases?

1. the Milankovitch cycles
2. volcanoes
3. solar intensity
4. burning of fossil fuels

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2.12: CRITICAL THINKING QUESTIONS

14.

Ecologists often collaborate with other researchers interested in ecological questions. Describe the levels of ecology that would be easier for collaboration because of the similarities of questions asked. What levels of ecology might be more difficult for collaboration?

15.

The population is an important unit in ecology as well as other biological sciences. How is a population defined, and what are the strengths and weaknesses of this definition? Are there some species that at certain times or places are not in populations?

16.

Compare and contrast ocean upwelling and spring and fall turnovers.

17.

Many endemic species are found in areas that are geographically isolated. Suggest a plausible scientific explanation for why this is so.

18.

The extremely low precipitation of subtropical desert biomes might lead one to expect fire to be a major disturbance factor; however, fire is more common in the temperate grassland biome than in the subtropical desert biome. Why is this?

19.

In what ways are the subtropical desert and the arctic tundra similar?

20.

Scientists have discovered the bodies of humans and other living things buried in bogs for hundreds of years, but not yet decomposed. Suggest a possible biological explanation for why such bodies are so well-preserved.

21.

Describe the conditions and challenges facing organisms living in the intertidal zone.

22.

Compare and contrast how natural- and human-induced processes have influenced global climate change.

23.

Predict possible consequences if carbon emissions from fossil fuels continue to rise.

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CHAPTER OVERVIEW

3: THE EVOLUTION OF POPULATIONS

Natural selection is one of the most dominant evolutionary forces. Natural selection acts to promote traits and behaviors that increase an organism's chances of survival and reproduction, while eliminating those traits and behaviors that are to the organism's detriment. But natural selection can only, as its name implies, select—it cannot create. The introduction of novel traits and behaviors falls on the shoulders of another evolutionary force—mutation. Mutation and other sources of variation among individuals, as well as the evolutionary forces that act upon them, alter populations and species. This combination of processes has led to the world of life we see today.

3.1: Introduction
3.2: Population Evolution
3.3: Population Genetics
3.4: Adaptive Evolution
3.5: Key Terms
3.6: Chapter Summary
3.7: Visual Connection Questions
3.8: Review Questions
3.9: Critical Thinking Questions

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3.1: INTRODUCTION



Figure 19.1 Living things may be single-celled or complex, multicellular organisms. They may be plants, animals, fungi, bacteria, or archaea. This diversity results from evolution. (credit "wolf": modification of work by Gary Kramer; credit "coral": modification of work by William Harrigan, NOAA; credit "river": modification of work by Vojtěch Dostál; credit "fish" modification of work by Christian Mehlführer; credit "mushroom": modification of work by Cory Zanker; credit "tree": modification of work by Joseph Kranak; credit "bee": modification of work by Cory Zanker)

CHAPTER OUTLINE

19.1 Population Evolution
19.2 Population Genetics
19.3 Adaptive Evolution

All life on Earth is related. Evolutionary theory states that humans, beetles, plants, and bacteria all share a common ancestor, but that millions of years of evolution have shaped each of these organisms into the forms we see today. Scientists consider evolution a key concept to understanding life. It is one of the most dominant evolutionary forces. Natural selection acts to promote traits and behaviors that increase an organism's chances of survival and reproduction, while eliminating those traits and behaviors that are detrimental to the organism. However, natural selection can only, as its name implies, select—it cannot create. We can attribute novel traits and behaviors to another evolutionary force—mutation. Mutation and other sources of variation among individuals, as well as the evolutionary forces that act upon them, alter populations and species. This combination of processes has led to the world of life we see today.

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3.2: POPULATION EVOLUTION

LEARNING OBJECTIVES

By the end of this section, you will be able to do the following:

- Define population genetics and describe how scientists use population genetics in studying population evolution
- Define the Hardy-Weinberg principle and discuss its importance

People did not understand the mechanisms of inheritance, or genetics, at the time Charles Darwin and Alfred Russel Wallace were developing their idea of natural selection. This lack of knowledge was a stumbling block to understanding many aspects of evolution. The predominant (and incorrect) genetic theory of the time, blending inheritance, made it difficult to understand how natural selection might operate. Darwin and Wallace were unaware of the Austrian monk Gregor Mendel's 1866 publication "Experiments in Plant Hybridization", which came out not long after Darwin's book, *On the Origin of Species*. Scholars rediscovered Mendel's work 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. However, over the next few decades scientists integrated genetics and evolution in what became known as the modern synthesis—the coherent understanding of the relationship between natural selection and genetics that took shape by the 1940s. Generally, this concept is accepted today. In short, the modern synthesis describes how evolutionary processes, 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 population change over time (microevolution), with the processes that gave rise to new species and higher taxonomic groups with widely divergent characters, called (macroevolution).

EVERYDAY CONNECTION

EVERYDAY CONNECTION

Evolution and Flu VaccinesEvery fall, the media starts reporting on flu vaccinations and potential outbreaks. Scientists, health experts, and institutions determine recommendations for different parts of the population, predict optimal production and inoculation schedules, create vaccines, and set up clinics to provide inoculations. You may think of the annual flu shot as media hype, an important health protection, or just a briefly uncomfortable prick in your arm. However, do you think of it in terms of evolution?

The media hype of annual flu shots is scientifically grounded in our understanding of evolution. Each year, scientists across the globe strive to predict the flu strains that they anticipate as most widespread and harmful in the coming year. They base this knowledge on how flu strains have evolved over time and over the past few flu seasons. Scientists then work to create the most effective vaccine to combat those selected strains. Pharmaceutical companies produce hundreds of millions of doses in a short period in order to provide vaccinations to key populations at the optimal time.

Because viruses, like the flu, evolve very quickly (especially in evolutionary time), this poses quite a challenge. Viruses mutate and replicate at a fast rate, so the vaccine developed to protect against last year's flu strain may not provide the protection one needs against the coming year's strain. Evolution of these viruses means continued adaptations to ensure survival, including adaptations to survive previous vaccines.

POPULATION GENETICS

Recall that a gene for a particular character may have several alleles, or variants, that code for different traits associated with that character. For example, in the ABO blood type system in humans, three alleles determine the particular blood-type carbohydrate on the surface of red blood cells. Each individual in a population of diploid organisms can only carry two alleles for a particular gene, but more than two may be present in the individuals that comprise the population. Mendel followed alleles as they were inherited from parent to offspring. In the early twentieth century, biologists in the area of population genetics began to study how selective forces change a population through changes in allele and genotypic frequencies.

The allele frequency (or gene frequency) is the rate at which a specific allele appears within a population. Until now we have discussed evolution as a change in the characteristics of a population of organisms, but behind that phenotypic change is genetic change. In population genetics, scientists define the term evolution as a change in the allele's frequency in a population. Using the ABO blood type system as an example, the frequency of one of the alleles, I^A, is the number of copies of that allele divided by all the copies of the ABO gene in the population. For example, a study in Jordan[1] found a frequency of I^A to be 26.1 percent. The I^B and I^0 alleles comprise 13.4 percent and 60.5 percent of the alleles respectively, and all of the frequencies added up to 100 percent. A change in this frequency over time would constitute evolution in the population.

The allele frequency within a given population can change depending on environmental factors; therefore, certain alleles become more widespread than others during the natural selection process. Natural selection can alter the population's genetic makeup. An example is if a given allele confers a phenotype that allows an individual to better survive or have more offspring. Because many of those offspring will also carry the beneficial allele, and often the corresponding phenotype, they will have more offspring of their own that also carry the allele, thus, perpetuating the cycle. Over time, the allele will spread throughout the population. Some alleles will quickly become fixed in this way, meaning that every individual of the population will carry the allele, while detrimental mutations may be swiftly eliminated if derived from a dominant allele from the gene pool. The gene pool is the sum of all the alleles in a population.

Sometimes, allele frequencies within a population change randomly with no advantage to the population over existing allele frequencies. We call this phenomenon genetic drift. Natural selection and genetic drift usually occur simultaneously in populations and are not isolated events. It is hard to determine which process dominates because it is often nearly impossible to determine the cause of change in allele frequencies at each occurrence. We call an event that initiates an allele frequency change in an isolated part of the population, which is not typical of the original population, the founder effect. Natural selection, random drift, and founder effects can lead to significant changes in a population's genome.

HARDY-WEINBERG PRINCIPLE OF EQUILIBRIUM

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. The Hardy-Weinberg principle assumes an infinitely large population and conditions with no mutations, migration, emigration, or selective pressure for or against genotype. While no population can satisfy those conditions, the principle offers a useful model against which to compare real population changes.

Working under this theory, population geneticists represent different alleles as different variables in their mathematical models. The variable p, for example, often represents the frequency of a particular allele, say Y for the trait of yellow in Mendel's peas, while the variable q represents the frequency of y alleles that confer the color green. If these are the only two possible alleles for a given locus in the population, $p + q = 1$. In other words, all the p alleles and all the q alleles comprise all of the alleles for that locus in the population.

However, what ultimately interests most biologists is not the frequencies of different alleles, but the frequencies of the resulting genotypes, known as the population's genetic structure, from which scientists can surmise phenotype distribution. If we observe the phenotype, we can know only the homozygous recessive allele's genotype. The 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. In the above scenario, 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 (Figure 19.2). In other words, the frequency of pp individuals is simply p^2; the frequency of pq individuals is 2pq; and the frequency of qq individuals is q^2. Again, if p and q are the only two possible alleles for a given trait in the population, these genotypes frequencies will sum to one: $p^2 + 2pq + q^2 = 1$.

VISUAL CONNECTION

VISUAL CONNECTION

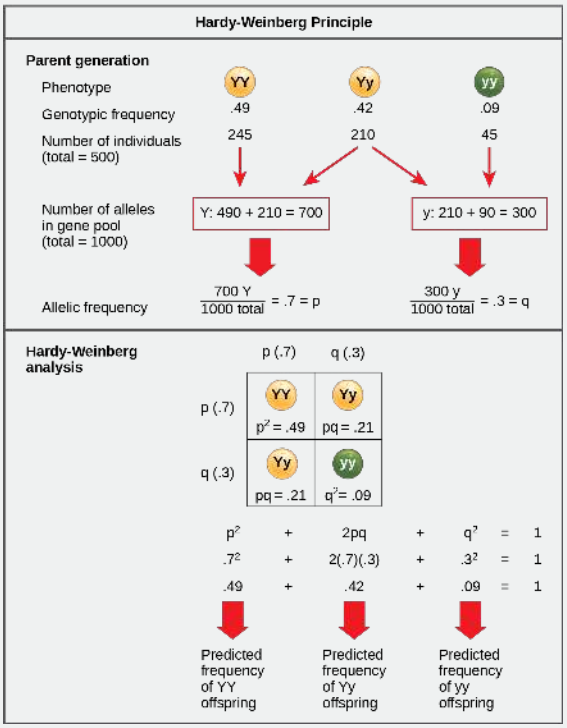


Figure 19.2 When populations are in the Hardy-Weinberg equilibrium, the allelic frequency is stable from generation to generation and we can determine the allele distribution from the Hardy-Weinberg equation. If the allelic frequency measured in the field differs from the predicted value, scientists can make inferences about what evolutionary forces are at play.

In plants, violet flower color (V) is dominant over white (v). If p = 0.8 and 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?

In theory, if a population is at equilibrium—that is, there are no evolutionary forces acting upon it—generation after generation would have the same gene pool and genetic structure, and these equations would all hold true all of the time. Of course, even Hardy and Weinberg recognized that no natural population is immune to evolution. Populations in nature are constantly changing in genetic makeup due to drift, mutation, possibly migration, and selection. As a result, the only way to determine the exact distribution of phenotypes in a population is to go out and count them. However, the Hardy-Weinberg principle gives scientists a mathematical baseline of a non-evolving population to which they can compare evolving populations and thereby infer what evolutionary forces might be at play. If the frequencies of alleles or genotypes deviate from the value expected from the Hardy-Weinberg equation, then the population is evolving.

LINK TO LEARNING

LINK TO LEARNING

Use this online calculator to determine a population's genetic structure.

FOOTNOTES

- 1Sahar S. Hanania, Dhia S. Hassawi, and Nidal M. Irshaid, “Allele Frequency and Molecular Genotypes of ABO Blood Group System in a Jordanian Population,” *Journal of Medical Sciences* 7 (2007): 51-58, doi:10.3923/jms.2007.51.58.

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3.3: POPULATION GENETICS

LEARNING OBJECTIVES

By the end of this section, you will be able to do the following:

- Describe the different types of variation in a population
- Explain why only natural selection can act upon heritable variation
- Describe genetic drift and the bottleneck effect
- Explain how each evolutionary force can influence a population's allele frequencies

A population's individuals often display different phenotypes, or express different alleles of a particular gene, which scientists refer to as polymorphisms. We call populations with two or more variations of particular characteristics polymorphic. A number of factors, including the population's genetic structure and the environment (Figure 19.3) influence population variation, the distribution of phenotypes among individuals. Understanding phenotypic variation sources in a population is important for determining how a population will evolve in response to different evolutionary pressures.



Figure 19.3 The distribution of phenotypes in this litter of kittens illustrates population variation. (credit: Pieter Lanser)

GENETIC VARIANCE

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, while deleterious alleles may not. 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 body builder. If there is a genetic basis for the ability to run fast, on the other hand, a parent may pass this to a child.

LINK TO LEARNING

LINK TO LEARNING

Before Darwinian evolution became the prevailing theory of the field, French naturalist Jean-Baptiste Lamarck theorized that organisms could inherit acquired traits. While the majority of scientists have not supported this hypothesis, some have recently begun to realize that Lamarck was not completely wrong. Visit this site to learn more.

Heritability is the fraction of phenotype variation that we can attribute to genetic differences, or genetic variance, among individuals in a population. The greater the heritability of a population's phenotypic variation, the more susceptible it is to the evolutionary forces that act on heritable variation.

We call the diversity of alleles and genotypes within a population genetic variance. 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 possible. This also helps reduce associated risks of 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 maintains itself 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 that scientists call inbreeding depression.

Changes in allele frequencies that we identify in a population can shed light on how it is evolving. In addition to natural selection, there are other evolutionary forces that could be in play: genetic drift, gene flow, mutation, nonrandom mating, and environmental variances.

GENETIC DRIFT

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.

Another way a population's allele and genotype frequencies can change is genetic drift (Figure 19.4), which is simply the effect of chance. By chance, 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).

VISUAL CONNECTION

VISUAL CONNECTION

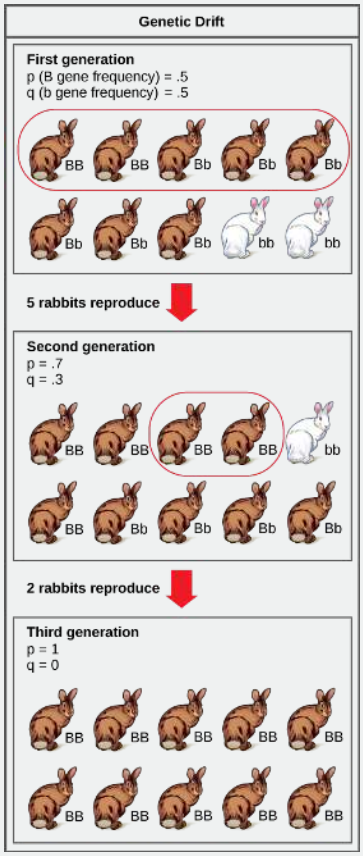


Figure 19.4 Genetic drift in a population can lead to eliminating an allele from a population by chance. In this example, rabbits with the brown coat color allele (*B*) are dominant over rabbits with the white coat color allele (*b*). In the first generation, the two alleles occur with equal frequency in the population, resulting in p and q values of .5. Only half of the individuals reproduce, resulting in a second generation with p and q values of .7 and .3, respectively. Only two individuals in the second generation reproduce, and by chance these individuals are homozygous dominant for brown coat color. As a result, in the third generation the recessive *b* allele is lost.

Do you think genetic drift would happen more quickly on an island or on the mainland?

Small populations are more susceptible to the forces of genetic drift. Large populations, alternatively, are buffered against the effects of chance. If one individual of a population of 10 individuals happens to die at a young age before it leaves 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's only 1 percent of the overall gene pool; therefore, it is much less impactful on the population's genetic structure.

LINK TO LEARNING

LINK TO LEARNING

Go to this site to watch an animation of random sampling and genetic drift in action.

Natural events, such as an earthquake disaster that kills—at random—a large portion of the population, can magnify genetic drift. Known as the bottleneck effect, it results in suddenly wiping out a large portion of the gene pool (Figure 19.5). At once, the survivors' genetic structure becomes the entire population's genetic structure, which may be very different from the pre-disaster population.

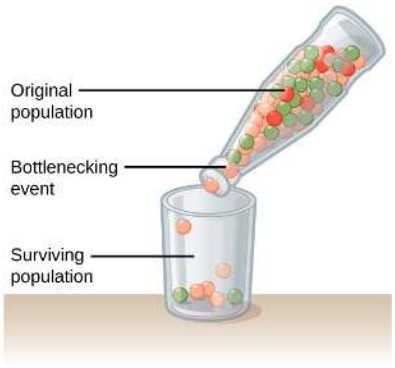


Figure 19.5 A chance event or catastrophe can reduce the genetic variability within a population.

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 physical barrier divides a population. In this situation, those individuals are an unlikely representation 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. Researchers believe that the founder effect was 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 is probably because 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.[2]

LINK TO LEARNING

LINK TO LEARNING

Watch this short video to learn more about the founder and bottleneck effects.

Click to view content

SCIENTIFIC METHOD CONNECTION

SCIENTIFIC METHOD CONNECTION

Testing the Bottleneck Effect

Question: How do natural disasters affect a population's genetic structure?

Background: When an earthquake or hurricane suddenly wipes out much of a population, the surviving individuals are usually a random sampling of the original group. As a result, the population's genetic makeup can change dramatically. We call this phenomenon the bottleneck effect.

Hypothesis: Repeated natural disasters will yield different population genetic structures; therefore, each time one runs this experiment the results will vary.

Test the hypothesis: Count out the original population 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 1/3 of the bottle's contents into a bowl. This represents the surviving individuals after a natural disaster kills a majority 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 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 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 Mississippi Gulf Coast? How do the seabirds that live on the beach fare?

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 19.6). 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 population's gene structure, but it can also introduce new genetic variation to populations in different geological locations and habitats.

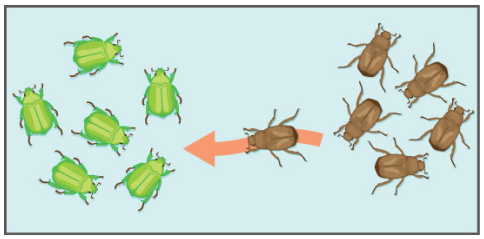


Figure 19.6 Gene flow can occur when an individual travels from one geographic location to another.

MUTATION

Mutations are changes to an organism’s DNA and are an important driver of diversity in populations. Species evolve because of mutations accumulating over time. The appearance of new mutations is the most common way to introduce novel genotypic and phenotypic variance. Some mutations are unfavorable or harmful and are quickly eliminated from the population by natural selection. 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. Some can have a dramatic effect on a gene and the resulting phenotype.

NONRANDOM MATING

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 peahens may prefer peacocks with bigger, brighter tails. Natural selection picks traits that lead to more mating selections for an individual. 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 vast 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.

ENVIRONMENTAL VARIANCE

Genes are not the only players involved in determining population variation. Other factors, such as the environment (Figure 19.7) also influence phenotypes. A beachgoer is likely to have darker skin than a city dweller, for example, due to regular exposure to the sun, an environmental factor. For some species, the environment determines some major characteristics, such as gender. 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 19.7 The temperature at which the eggs are incubated determine the American alligator's (*Alligator mississippiensis*) sex. Eggs incubated at 30°C produce females, and eggs incubated at 33°C produce males. (credit: Steve Hillebrand, USFWS)

Geographic separation between populations can lead to differences in the phenotypic variation between those populations. We see such geographical variation between most populations and it can be significant. We can observe one type of geographic variation, a cline, as given species' populations vary gradually across an ecological gradient. 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 a latitudinal cline. Alternatively, flowering plants tend to bloom at different times depending on where they are along a mountain slope. This is an altitudinal cline.

If there is gene flow between the populations, the individuals will likely show gradual differences in phenotype along the cline. Restricted gene flow, alternatively can lead to abrupt differences, even speciation.

FOOTNOTES

- 2A. 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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3.4: ADAPTIVE EVOLUTION

LEARNING OBJECTIVES

By the end of this section, you will be able to do the following:

- Explain the different ways natural selection can shape populations
- Describe how these different forces can lead to different outcomes in terms of the population variation

Natural selection acts on the population's heritable traits: selecting for beneficial alleles that allow for environmental adaptation, and thus increasing their frequency in the population, while selecting against deleterious alleles and thereby decreasing their frequency. Scientists call this process adaptive evolution. Natural selection acts on entire organisms, not on an individual allele within the organism. An individual may carry a very beneficial genotype with a resulting phenotype that, for example, increases the ability to reproduce (fecundity), but if that same individual also carries an allele that results in a fatal childhood disease, that fecundity phenotype will not pass to the next generation because the individual will not live to reach reproductive age. Natural selection acts at the individual's level. It selects for individuals with greater contributions to the gene pool of the next generation. Scientists call this an organism's evolutionary (Darwinian) fitness.

Fitness is often quantifiable and is measured by scientists in the field. However, it is not an individual's absolute fitness that counts, but rather how it compares to the other organisms in the population. Scientists call this concept relative fitness, which allows researchers to determine which individuals are contributing additional offspring to the next generation, and thus, how the population might evolve.

There are several ways selection can affect population variation: stabilizing selection, directional selection, diversifying selection, frequency-dependent selection, and sexual selection. As natural selection influences the allele frequencies in a population, individuals can either become more or less genetically similar and the phenotypes can become more similar or more disparate.

STABILIZING SELECTION

If natural selection favors an average phenotype, selecting against extreme variation, the population will undergo stabilizing selection (Figure 19.8). In a mouse population that live in the woods, for example, natural selection is likely to favor mice that best blend in with the forest floor and are less likely for predators to spot. Assuming the ground is a fairly consistent shade of brown, those mice whose fur is most closely matched to that color will be most likely to survive and reproduce, passing on their genes for their brown coat. Mice that carry alleles that make them a bit lighter or a bit darker will stand out against the ground and be more likely to fall victim to predation. As a result of this selection, the population's genetic variance will decrease.

DIRECTIONAL SELECTION

When the environment changes, populations will often undergo directional selection (Figure 19.8), which selects for phenotypes at one end of the spectrum of existing variation. A classic example of this type of selection is the evolution of the peppered moth 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. However, 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 moth's melanic form increased because they had a higher survival rate in habitats affected by air pollution because their darker coloration blended with the sooty trees. Similarly, the hypothetical mouse population may evolve to take on a different coloration if something were to cause the forest floor where they live to change color. The result of this type of selection is a shift in the population's genetic variance toward the new, fit phenotype.

LINK TO LEARNING

LINK TO LEARNING

In science, we sometimes believe some things are true, and then new information becomes available that changes our understanding. The peppered moth story is an example: some scientists recently have questioned the facts behind the selection toward darker moths. Read this article to learn more.

DIVERSIFYING SELECTION

Sometimes two or more distinct phenotypes can each have their advantages for natural selection, while the intermediate phenotypes are, on average, less fit. Scientists call this diversifying selection (Figure 19.8) We see this in many animal populations that have multiple male forms. Large, dominant alpha males use brute force to obtain mates, 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, who

can’t 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 mouse population 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, alternatively would not blend in with either the grass or the sand, and thus predators would most likely eat them. The result of this type of selection is increased genetic variance as the population becomes more diverse.

VISUAL CONNECTION

VISUAL CONNECTION

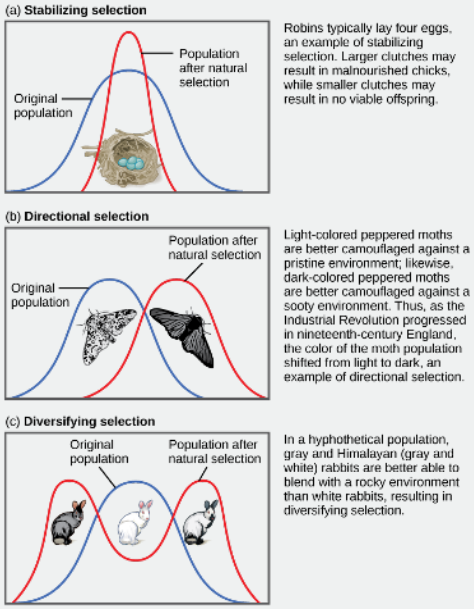


Figure 19.8 Different types of natural selection can impact the distribution of phenotypes within a population. In (a) stabilizing selection, an average phenotype is favored. In (b) directional selection, a change in the environment shifts the spectrum of observed phenotypes. In (c) diversifying selection, two or more extreme phenotypes are selected for, while the average phenotype is selected against.

In recent years, factories have become cleaner, and release less soot into the environment. What impact do you think this has had on the distribution of moth color in the population?

FREQUENCY-DEPENDENT SELECTION

Another type of selection, frequency-dependent selection, favors phenotypes that are either common (positive frequency-dependent selection) or rare (negative frequency-dependent selection). We can observe an interesting example of this type of selection in a unique group of Pacific Northwest lizards. 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. Yellow males (Figure 19.9) are the smallest, and look a bit like females, which allows 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. That is, 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 19.9 A yellow-throated side-blotched lizard 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. (credit: “tinyfroglet”/Flickr)

In this scenario, natural selection favors orange males when blue males dominate the population. 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 predominate, and then yellow males will begin to rise in frequency. Once yellow males comprise a majority of the population, blue males will be selected. Finally, when blue males become common, orange males once again will be favored.

Negative frequency-dependent selection serves to increase the population’s genetic variance by selecting for rare phenotypes; whereas, positive frequency-dependent selection usually decreases genetic variance by selecting for common phenotypes.

SEXUAL SELECTION

Males and females of certain species are often quite different from one another in ways beyond the reproductive organs. Males are often larger, for example, and display many elaborate colors and adornments, like the peacock’s tail, while females tend to be smaller and duller in decoration. We call such differences sexual dimorphisms (Figure 19.10), which arise in many populations, particularly animal populations, where there is more variance in the male's reproductive success than that of the females. That is, some males—often the bigger, stronger, or more decorated males—obtain the vast majority of the total matings, while others receive none. This can occur because the males are better at fighting off other males, or because females will choose to mate with the bigger or more decorated males. In either case, this variation in reproductive success generates a strong selection pressure among males to obtain those matings, resulting in the evolution of bigger body size and elaborate ornaments to attract the females’ attention. Females, however, tend to achieve a handful of selected matings; therefore, they are more likely to select more desirable males.

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

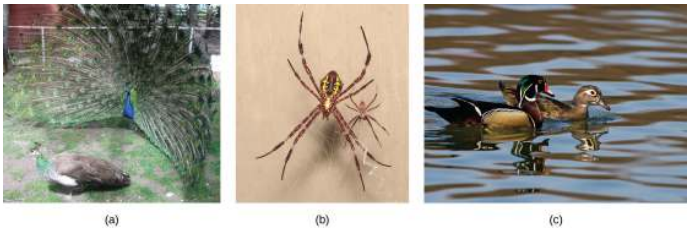


Figure 19.10 Sexual dimorphism in (a) peacocks and peahens, (b) *Argiope appensa* spiders (the female spider is the large one), and in (c) wood ducks. (credit “spiders”: modification of work by “Sanba38”/Wikimedia Commons; credit “duck”: modification of work by Kevin Cole)

We call the selection pressures on males and females to obtain matings sexual selection. It can result in developing secondary sexual characteristics that do not benefit the individual’s likelihood of survival but help to maximize its reproductive success. Sexual selection can be so strong that it selects traits that are actually detrimental to the individual’s survival. Think, once again, about the peacock’s tail. While it is beautiful and the male with the largest, most colorful tail is more likely to win the female, it is not the most practical appendage. In addition to greater visibility to predators, it makes the males slower in their attempted escapes. There is some evidence that this risk is why females like the big tails in the first place. The speculation is that large tails carry risk, and only the best males survive that risk: the bigger the tail, the more fit the male. We call this the handicap principle.

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. Although one may argue that females should not be picky 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.

LINK TO LEARNING

LINK TO LEARNING

In 1915, biologist Ronald Fisher proposed another model of sexual selection: the Fisherian runaway model, which suggests that selection of certain traits is a result of sexual preference.

In both the handicap principle and the good genes hypothesis, the trait is an honest signal of the males' quality, thus giving females a way to find the fittest mates— males that will pass the best genes to their offspring.

NO PERFECT ORGANISM

Natural selection is a driving force in evolution and can generate populations that are better adapted to survive and successfully reproduce in their environments. However, natural selection cannot produce the perfect organism. Natural selection can only select on existing variation in the population. It does not create anything from scratch. Thus, it is limited by a population's existing genetic variance and whatever new alleles arise through mutation and gene flow.

Natural selection is also limited because it works at the individual, not allele level, and some alleles are linked due to their physical proximity in the genome, making them more likely to pass on together (linkage disequilibrium). Any given individual may carry some beneficial and some unfavorable alleles. It is the alleles' net effect, or the organism's fitness, upon which natural selection can act. As a result, good alleles can be lost if individuals who carry them also have several overwhelmingly bad alleles. Likewise, bad alleles can be kept if individuals who have enough good alleles to result in an overall fitness benefit carry them.

Furthermore, natural selection can be constrained by the relationships between different polymorphisms. One morph may confer a higher fitness than another, but may not increase in frequency because going from the less beneficial to the more beneficial trait would require going through a less beneficial phenotype. Think back to the mice that live at the beach. Some are light-colored and blend in with the sand, while others are dark and blend in with the patches of grass. The dark-colored mice may be, overall, more fit than the light-colored mice, and at first glance, one might expect the light-colored mice to be selected for a darker coloration. However, remember that the intermediate phenotype, a medium-colored coat, is very bad for the mice—they cannot blend in with either the sand or the grass and predators are more likely to eat them. As a result, the light-colored mice would not be selected for a dark coloration because those individuals who began moving in that direction (began selection for a darker coat) would be less fit than those that stayed light.

Finally, it is important to understand that not all evolution is adaptive. While natural selection selects the fittest individuals and often results in a more fit population overall, other forces of evolution, including genetic drift and gene flow, often do the opposite: introducing deleterious alleles to the population's gene pool. Evolution has no purpose—it is not changing a population into a preconceived ideal. It is simply the sum of the various forces that we have described in this chapter and how they influence the population's genetic and phenotypic variance.

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3.5: KEY TERMS

adaptive evolution
increase in frequency of beneficial alleles and decrease in deleterious alleles due to selection

allele frequency
(also, gene frequency) rate at which a specific allele appears within a population

assortative mating
when individuals tend to mate with those who are phenotypically similar to themselves

bottleneck effect
magnification of genetic drift as a result of natural events or catastrophes

cline
gradual geographic variation across an ecological gradient

directional selection
selection that favors phenotypes at one end of the spectrum of existing variation

diversifying selection
selection that favors two or more distinct phenotypes

evolutionary fitness
(also, Darwinian fitness) individual's ability to survive and reproduce

founder effect
event that initiates an allele frequency change in part of the population, which is not typical of the original population

frequency-dependent selection
selection that favors phenotypes that are either common (positive frequency-dependent selection) or rare (negative frequency-dependent selection)

gene flow
flow of alleles in and out of a population due to the individual or gamete migration

gene pool
all the alleles that the individuals in the population carry

genetic drift
effect of chance on a population's gene pool

genetic structure
distribution of the different possible genotypes in a population

genetic variance
diversity of alleles and genotypes in a population

geographical variation
differences in the phenotypic variation between populations that are separated geographically

good genes hypothesis
theory of sexual selection that argues individuals develop impressive ornaments to show off their efficient metabolism or ability to fight disease

handicap principle

theory of sexual selection that argues only the fittest individuals can afford costly traits

heritability
fraction of population variation that can be attributed to its genetic variance

honest signal
trait that gives a truthful impression of an individual's fitness

inbreeding
mating of closely related individuals

inbreeding depression
increase in abnormalities and disease in inbreeding populations

macroevolution
broader scale evolutionary changes that scientists see over paleontological time

microevolution
changes in a population's genetic structure

modern synthesis
overarching evolutionary paradigm that took shape by the 1940s and scientists generally accept today

nonrandom mating
changes in a population's gene pool due to mate choice or other forces that cause individuals to mate with certain phenotypes more than others

population genetics
study of how selective forces change the allele frequencies in a population over time

population variation
distribution of phenotypes in a population

relative fitness
individual's ability to survive and reproduce relative to the rest of the population

selective pressure
environmental factor that causes one phenotype to be better than another

sexual dimorphism
phenotypic difference between a population's males and females

stabilizing selection
selection that favors average phenotypes

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3.6: CHAPTER SUMMARY

19.1 POPULATION EVOLUTION

The modern synthesis of evolutionary theory grew out of the cohesion of Darwin's, Wallace's, and Mendel's thoughts on evolution and heredity, along with the more modern study of population genetics. It describes the evolution of populations and species, from small-scale changes among individuals to large-scale changes over paleontological time periods. To understand how organisms evolve, scientists can track populations' allele frequencies over time. If they differ from generation to generation, scientists can conclude that the population is not in Hardy-Weinberg equilibrium, and is thus evolving.

19.2 POPULATION GENETICS

Both genetic and environmental factors can cause phenotypic variation in a population. Different alleles can confer different phenotypes, and different environments can also cause individuals to look or act differently. Only those differences encoded in an individual's genes, however, can pass to its offspring and, thus, be a target of natural selection. Natural selection works by selecting for alleles that confer beneficial traits or behaviors, while selecting against those for deleterious qualities. Genetic drift stems from the chance occurrence that some individuals in the gene line have more offspring than others. When individuals leave or join the population, allele frequencies can change as a result of gene flow. Mutations to an individual's DNA may introduce new variation into a population. Allele frequencies can also alter when individuals do not randomly mate with others in the group.

19.3 ADAPTIVE EVOLUTION

Because natural selection acts to increase the frequency of beneficial alleles and traits while decreasing the frequency of deleterious qualities, it is adaptive evolution. Natural selection acts at the individual level, selecting for those that have a higher overall fitness compared to the rest of the population. If the fit phenotypes are those that are similar, natural selection will result in stabilizing selection, and an overall decrease in the population's variation. Directional selection works to shift a population's variance toward a new, fit phenotype, as environmental conditions change. In contrast, diversifying selection results in increased genetic variance by selecting for two or more distinct phenotypes.

Other types of selection include frequency-dependent selection, in which individuals with either common (positive frequency-dependent selection) or rare (negative frequency-dependent selection) are selected. Finally, sexual selection results from one sex having more variance in the reproductive success than the other. As a result, males and females experience different selective pressures, which can often lead to the evolution of phenotypic differences, or sexual dimorphisms, between the two.

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3.7: VISUAL CONNECTION QUESTIONS

1.

Figure 19.2 In plants, violet flower color (V) is dominant over white (v). If p = .8 and 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?

2.

Figure 19.4 Do you think genetic drift would happen more quickly on an island or on the mainland?

3.

Figure 19.8 In recent years, factories have become cleaner, and less soot is released into the environment. What impact do you think this has had on the distribution of moth color in the population?

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3.8: REVIEW QUESTIONS

4.

What is the difference between micro- and macroevolution?

1. Microevolution describes the evolution of small organisms, such as insects, while macroevolution describes the evolution of large organisms, like people and elephants.
2. Microevolution describes the evolution of microscopic entities, such as molecules and proteins, while macroevolution describes the evolution of whole organisms.
3. Microevolution describes the evolution of organisms in populations, while macroevolution describes the evolution of species over long periods of time.
4. Microevolution describes the evolution of organisms over their lifetimes, while macroevolution describes the evolution of organisms over multiple generations.

5.

Population genetics is the study of:

1. how selective forces change the allele frequencies in a population over time
2. the genetic basis of population-wide traits
3. whether traits have a genetic basis
4. the degree of inbreeding in a population

6.

Which of the following populations is not in Hardy-Weinberg equilibrium?

1. a population with 12 homozygous recessive individuals (yy), 8 homozygous dominant individuals (YY), and 4 heterozygous individuals (Yy)
2. a population in which the allele frequencies do not change over time
3. $p^2 + 2pq + q^2 = 1$
4. a population undergoing natural selection

7.

One of the original Amish colonies rose from a ship of colonists that came from Europe. The ship's captain, who had polydactyly, a rare dominant trait, was one of the original colonists. Today, we see a much higher frequency of polydactyly in the Amish population. This is an example of:

1. natural selection
2. genetic drift
3. founder effect
4. b and c

8.

When male lions reach sexual maturity, they leave their group in search of a new pride. This can alter the allele frequencies of the population through which of the following mechanisms?

1. natural selection
2. genetic drift
3. gene flow
4. random mating

9.

Which of the following evolutionary forces can introduce new genetic variation into a population?

1. natural selection and genetic drift
2. mutation and gene flow
3. natural selection and nonrandom mating
4. mutation and genetic drift

10.

What is assortative mating?

1. when individuals mate with those who are similar to themselves

2. when individuals mate with those who are dissimilar to themselves
3. when individuals mate with those who are the most fit in the population
4. when individuals mate with those who are least fit in the population

11.

When closely related individuals mate with each other, or inbreed, the offspring are often not as fit as the offspring of two unrelated individuals. Why?

1. Close relatives are genetically incompatible.
2. The DNA of close relatives reacts negatively in the offspring.
3. Inbreeding can bring together rare, deleterious mutations that lead to harmful phenotypes.
4. Inbreeding causes normally silent alleles to be expressed.

12.

What is a cline?

1. the slope of a mountain where a population lives
2. the degree to which a mutation helps an individual survive
3. the number of individuals in the population
4. gradual geographic variation across an ecological gradient

13.

Which type of selection results in greater genetic variance in a population?

1. stabilizing selection
2. directional selection
3. diversifying selection
4. positive frequency-dependent selection

14.

When males and females of a population look or act differently, it is referred to as _____.

1. sexual dimorphism
2. sexual selection
3. diversifying selection
4. a cline

15.

The good genes hypothesis is a theory that explains what?

1. why more fit individuals are more likely to have more offspring
2. why alleles that confer beneficial traits or behaviors are selected for by natural selection
3. why some deleterious mutations are maintained in the population
4. why individuals of one sex develop impressive ornamental traits

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3.9: CRITICAL THINKING QUESTIONS

16.

Solve for the genetic structure of a population with 12 homozygous recessive individuals (yy), 8 homozygous dominant individuals (YY), and 4 heterozygous individuals (Yy).

17.

Explain the Hardy-Weinberg principle of equilibrium theory.

18.

Imagine you are trying to test whether a population of flowers is undergoing evolution. You suspect there is selection pressure on the color of the flower: bees seem to cluster around the red flowers more often than the blue flowers. In a separate experiment, you discover blue flower color is dominant to red flower color. In a field, you count 600 blue flowers and 200 red flowers. What would you expect the genetic structure of the flowers to be?

19.

Describe a situation in which a population would undergo the bottleneck effect and explain what impact that would have on the population's gene pool.

20.

Describe natural selection and give an example of natural selection at work in a population.

21.

Explain what a cline is and provide examples.

22.

Give an example of a trait that may have evolved as a result of the handicap principle and explain your reasoning.

23.

List the ways in which evolution can affect population variation and describe how they influence allele frequencies.

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CHAPTER OVERVIEW

4: POPULATION ECOLOGY

Community ecology is the study of the interactions between species in communities on many spatial and temporal scales, including the distribution, structure, abundance, demography, and interactions between coexisting populations. The primary focus of community ecology is on the interactions between populations as determined by specific genotypic and phenotypic characteristics.

4.1: Introduction

4.1.1: Species and Populations

4.2: Population Demography

4.3: Life Histories and Natural Selection

4.4: Environmental Limits to Population Growth

4.5: Population Dynamics and Regulation

4.6: Human Population Growth

4.7: Key Terms

4.8: Chapter Summary

4.9: Visual Connection Questions

4.10: Review Questions

4.11: Critical Thinking Questions

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4.1: INTRODUCTION



Figure 45.1 Asian carp jump out of the water in response to electrofishing. The Asian carp in the photograph on the right were harvested from the Little Calumet River in Illinois in May, 2010, using rotenone, a toxin often used as an insecticide, in an effort to learn more about the population of the species. (credit left image: modification of work by USGS; credit right image: modification of work by Lt. David French, USCG)

CHAPTER OUTLINE

45.1 Population Demography
45.2 Life Histories and Natural Selection
45.3 Environmental Limits to Population Growth
45.4 Population Dynamics and Regulation
45.5 Human Population Growth
45.6 Community Ecology
45.7 Behavioral Biology: Proximate and Ultimate Causes of Behavior

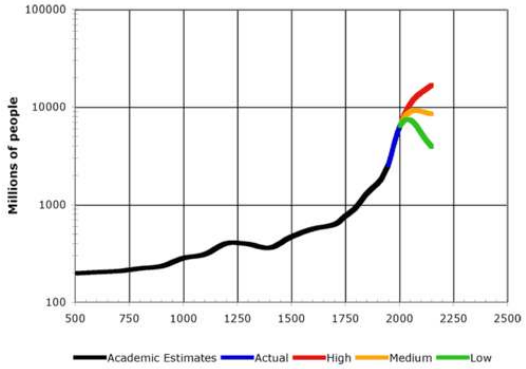
Imagine sailing down a river in a small motorboat on a weekend afternoon; the water is smooth and you are enjoying the warm sunshine and cool breeze when suddenly you are hit in the head by a 20-pound silver carp. This is now a risk on many rivers and canal systems in Illinois and Missouri because of the presence of Asian carp.

This fish—actually a group of species including the silver, black, grass, and big head carp—has been farmed and eaten in China for over 1000 years. It is one of the most important aquaculture food resources worldwide. In the United States, however, Asian carp is considered a dangerous invasive species that disrupts community structure and composition to the point of threatening native species.

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SECTION OVERVIEW

4.1.1: Species and Populations



World population from 500CE to 2150, based on UN (2004)[1] projections and U.S. census information[2], which are both applications of demography. No matter how much data is collected, unknown variables remain, so there are alternate possibilities for the future world population.

Species and populations are probably the two most commonly used ecology terms, but they are often difficult concepts to grasp. Throughout this chapter, they will be discussed in detail, expanding on the definitions from previous chapters and explaining why there are no universally acceptable definitions. Factors influencing population growth and ways to measure and predict population growth will also be subjects of specific focus. Populations can be affected by so many factors that it is almost impossible to take every variable into account. Demography is the statistical study of the age structure of a population, and it can be used in research to determine what is causing a decline or increase in population size over time. It is worthwhile to understand species concept and population growth even though they are such broad aspects, because they are fundamental to the science of ecology.

Species Concept

You should have familiarity with the species concept from biology and have been presented with this basic tenant of the biological sciences in Chapter 2 of this textbook. If need be,

- Reread Species (Follow links as necessary to understand concepts presented)

When initially considering the concept of species you may wonder why the division of organisms into species is necessary at all. According to Ernst W. Mayr, a renowned evolutionary biologist, the existence and reproductive characteristics of distinct species "prevents the production of too great a number of disharmonious incompatible gene combinations.[3]" Therefore, the basis for the existence of species is genotypic in nature. However, the existence of species is not traditionally doubted whereas the appropriate definition of a species is continually a topic of debate[4].



A mule is the infertile offspring of a horse and a donkey--an example of the gray area regarding interbreeding in the most common definition of a species.

Although a species can be defined in a number of different ways, the most common definition for a living species, suggested by Ernst W. Mayr, is *any group of individuals that can breed with themselves but not with any other group*. In other words, a species is any group of individuals that is "reproductively isolated.[5]" This definition, termed the Biological Species Concept, has limitations and exceptions[6]. Some animals that would not normally be considered part of the same species can breed with limited success. For example, a horse and a donkey can can breed to produce a mule offspring but, the mule is infertile. Accordingly, there is much debate regarding the amount of successful fertility required for two individuals to belong to the same species. There are also organisms that do not interbreed at all, but propagate through direct cloning of an individual, for example many plants and insects. Other definitions must be used to define the species of organisms such as these.

So, why is such a seemingly straight-forward concept so hard to define? One problem is that the definition of a species is used in many different contexts and undoubtedly fails to satisfy them all simultaneously. In particular, there has been a great deal of discontinuity between the application of the same species concept in a taxonomic or systematic sense and in an evolutionary sense[7]. In systematic biology species serve as fundamental units (taxa) for the description and historical progression of diversity. However, evolutionarily, species are considered only as elements of a process called speciation. Even without further knowledge of the differences between evolution and taxonomy, it is apparent that the concept of a species is used in different contexts by the two. This is just one example of the many obstacles encompassing the complex debate for a universally applicable definition of a species.

In fact, it seems, after years and years of debate, that it is impossible to attain a universally suitable definition for "species". As Pigliucci (2006, p. 50) points out:

> *...emotions have run high for decades on the "crucial" question of what a biological species is, while at the same time plenty of researchers have conducted brilliant studies on individual species and on the process of speciation, apparently unencumbered by the lack of a universally-agreed-upon definition of what species are...*

The species concept is basic to biology and therefore ecology, but it is really the **species population** that ecologists study.



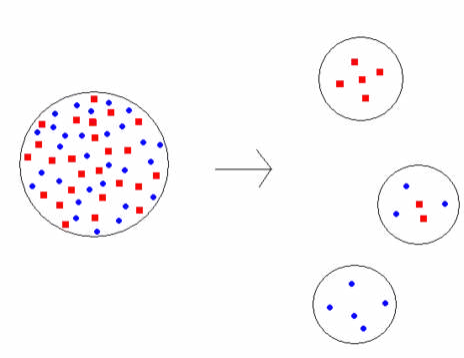
Part of a penguin (*Pygoscelis papua*) population in Antarctica

Population Biology

A *species population* is a discrete group of potentially interbreeding organisms in the same species in a given locality. Here, potential interbreeding has nothing to do with measures of fertility; instead it is a statement that all members of a population are potentially a part of a single gene pool. In a species population, there are many factors that interfere with an individual's fitness (its ability to survive and reproduce). Booth et al.(1995)[8] describes that an individual's fitness is increased with group living, also known as the Allee Effect, and that an individual's ability to survive will be increased by their size and rank. In this study, Booth shows that within the group of damselfish there was a greater chance for survival if they stayed in large groups. Within these groups the smaller individuals would benefit the most from the group living, but consequently the growth of these individuals was reduced, thus taking a longer time to reach a higher social status in the group. Reed et al. 2005 [9] support Booth's findings and also show that there is a linear relationship between log population size and population fitness. Reed suggests that "conservation efforts should ultimately aim at maintaining populations of several thousand individuals to ensure long-term persistence."

- Read Population The common use of the term in human demographics utilizes concepts and terms important to Population Biology

Diversity as a goal is split between species diversity and diversity within a population. An area that is filled with finches and owls and many species has species diversity. But if all the finches have very similar genes, or if the population has an inbreeding problem, there is not enough diversity within that population.



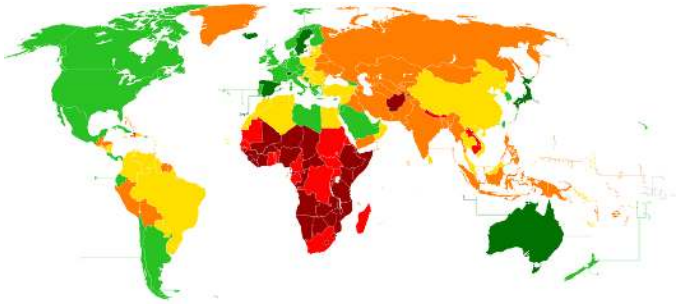
Limited diversity with separation.

When there is no diversity in the gene pool, serious effects can result. This may result from the Founder Effect. A major cause of Founder Effect is when a small part of a population has moved to an area with limited interaction with other populations from the same species. A well known example is the Old Order Amish in Pennsylvania. The Amish rarely interact with people outside of the community and rarely, if ever, marry outside of the population. With the limited genetic variation, genotypic and phenotypic problems are seen more frequently in the population compared with other human populations. The Amish carry a rare allele that causes polydactylism, in which there are extra fingers or toes. This recessive allele is carried by about 1 in every 14 Amish individuals compared to the outside population, where it is carried by about 1 in every 1000.

Another similar type of disturbance in a population is known as a Bottleneck. This disturbance occurs when a species is almost eliminated by human forces (hunting) or natural disasters. The cheetah is a prime example of a species with limited variation from a bottleneck. The cheetah's genetic make-up is so similar that a skin graft will not be rejected from one cheetah to another.

Even though the worldwide population of a species is potentially very large, not all individuals can interbreed due to obvious limitations such as separate continents, mountains or deserts, or great distances. A local population that does actually interbreed is called a neighborhood, or deme. So even though an overall population may not have inbreeding, neighborhoods could have potentially high inbreeding coefficients, which can increase the frequency of diseases or maintain a mutation in that species.

Population Growth



Population growth data can be used to determine and compare life expectancies of many regions.

Population growth is measured using time-specific life tables and age-specific life tables. Time-specific life tables are used for long-lived species, such as humans, and age-specific tables are used for short-lived species, such as annual plants and insects. Time-specific life tables assume equal birth rates for all age classes, and are useful for large populations. Age-specific life tables follow a cohort (a group of organisms of the same species and roughly similar ages) and require periodic sampling.

There are many types of useful information that studies of population growth can reveal, such as life histories for a population and life expectancies, such as in the map shown at right. Survivorship curves can also be determined by plotting the number of individuals of a cohort against time. Fecundity can be influenced by abiotic factors, such as precipitation (Milanovich et al. 2006).

Reproductive Rates

Closely related to the study of population growth is the reproductive rate of a population. Fecundity, m_x is the average number of offspring produced per breeding individual. A fecundity schedule is $R_0 = \sum l_x m_x$, where l_x is n_x/n_0 (the proportion surviving), m_x is the mean number of offspring per individual, and R_0 is the net reproductive rate of the population. If $R_0=1$, the population is stable. If $R_0<1$, the population is decreasing, and if $R_0>1$, the population is increasing.

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4.2: POPULATION DEMOGRAPHY

LEARNING OBJECTIVES

By the end of this section, you will be able to do the following:

- Describe how ecologists measure population size and density
- Describe three different patterns of population distribution
- Use life tables to calculate mortality rates
- Describe the three types of survivorship curves and relate them to specific populations

Populations are dynamic entities. A population consists of all of the individuals of a particular species that occur in a particular area and have the potential to interact with one another, 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 45.2, smaller organisms tend to be more densely distributed than larger organisms.

VISUAL CONNECTION

VISUAL CONNECTION

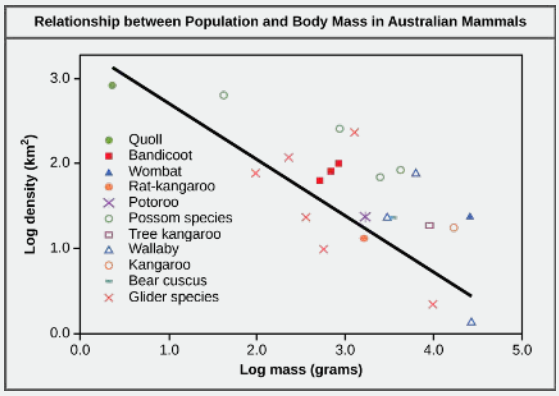


Figure 45.2 Australian mammals show a typical inverse relationship between population density and body size.

As this graph shows, population density typically decreases with increasing body size. Why do you think this is the case?

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. For immobile organisms such as plants, or for very small and slow-moving organisms, a quadrat may be used (Figure 45.3). 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. 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 to estimate the population size and 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. With giant redwoods, on the other hand, 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.

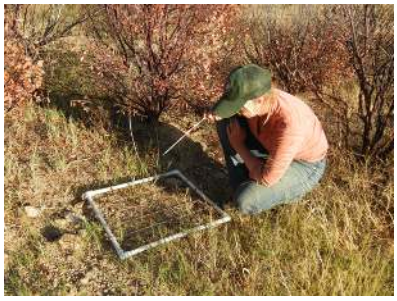


Figure 45.3 A scientist uses a quadrat to measure population size and density. (credit: NPS Sonoran Desert Network)

For mobile organisms, such as mammals, birds, or fish, scientists use a technique called mark and recapture. 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, researchers collect a new sample, including some individuals that are marked (recaptures) and some individuals that are unmarked (Figure 45.4).



Figure 45.4 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 estimate the population size (N) using the following equation:

$$\frac{\text{(number marked first catch x total number of second catch)}}{\text{number marked second catch}} = N$$

Using our example, the population size would be estimated at 400.

$$\frac{(80 \times 100)}{20} = 400$$

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, some animals may prefer to 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.

SPECIES DISTRIBUTION

In addition to measuring simple density, further information about a population can be obtained by looking at the distribution of the individuals. Species dispersion patterns (or distribution patterns) show 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 species live close together or far apart, and what patterns are evident when they are spaced apart.

Individuals in a population can be equally spaced apart, dispersed randomly with no predictable pattern, or clustered in groups. These are known as uniform, random, and clumped dispersion patterns, respectively (Figure 45.5). Uniform dispersion is observed in plants that secrete substances inhibiting the growth of nearby individuals (such as the release of toxic chemicals by the sage plant *Salvia leucophylla*, a phenomenon called allelopathy) and in animals like the penguin that maintain a defined territory. An example of random dispersion occurs with dandelion and other plants that have wind-dispersed seeds that germinate wherever they happen to fall in a favorable environment. A clumped dispersion may be seen in plants that drop their seeds straight to the ground, such as oak trees, or in animals that live in groups (schools of fish or herds of elephants). Clumped dispersions may also be a function of habitat heterogeneity. Thus, the dispersion 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.

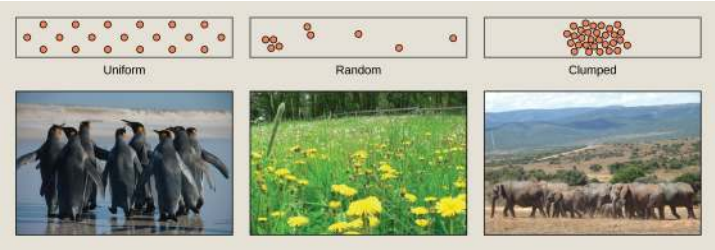


Figure 45.5 Species may have uniform, random, or clumped distribution. Territorial birds such as penguins tend to have uniform distribution. Plants such as dandelions with wind-dispersed seeds tend to be randomly distributed. Animals such as elephants that travel in groups exhibit clumped distribution. (credit a: modification of work by Ben Tubby; credit b: modification of work by Rosendahl; credit c: modification of work by Rebecca Wood)

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 45.1 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.

$$\text{mortality rate} = \frac{\text{number of individuals dying}}{\text{number of individuals surviving}} \text{x } 1000$$

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.

$$\text{mortality rate} = \frac{12}{776} \text{x } 1000 \approx 15.5$$

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 column E.

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

Table 45.1 This life table of *Ovis dalli* shows the number of deaths, number of survivors, mortality rate, and life expectancy at each age interval for the Dall mountain sheep.

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 45.6). 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.

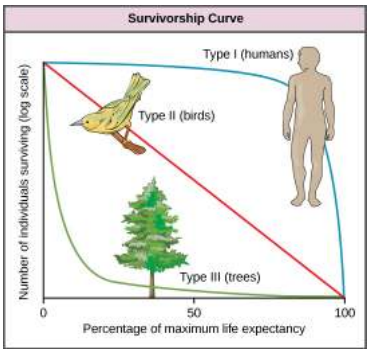


Figure 45.6 Survivorship curves show the distribution of individuals in a population according to age. Humans and most mammals have a Type I survivorship curve because death primarily occurs in the older years. Birds have a Type II survivorship curve, as death at any age is equally probable. Trees have a Type III survivorship curve because very few survive the younger years, but after a certain age, individuals are much more likely to survive.

FOOTNOTES

- 1Data Adapted from Edward S. Deevey, Jr., “Life Tables for Natural Populations of Animals,” *The Quarterly Review of Biology* 22, no. 4 (December 1947): 283-314.

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4.3: LIFE HISTORIES AND NATURAL SELECTION

LEARNING OBJECTIVES

By the end of this section, you will be able to do the following:

- Describe how life history patterns are influenced by natural selection
- Explain different life history patterns and how different reproductive strategies affect species' survival

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.

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 45.7a), 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 45.7b). 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 45.7c).



Figure 45.7 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)

LINK TO LEARNING

LINK TO LEARNING

Play this interactive PBS evolution-based mating game to learn more about reproductive strategies.

EVOLUTION CONNECTION

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 45.8).[2] 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 45.8 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.

FOOTNOTES

- 2Adapted 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.

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4.4: ENVIRONMENTAL LIMITS TO POPULATION GROWTH

LEARNING OBJECTIVES

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 45.9).

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:

$$\frac{\Delta N(\text{change in number})}{\Delta T(\text{change in time})} = B(\text{birth rate}) - D(\text{death rate})$$

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:

$$\frac{dN}{dT} = r_{max}N$$

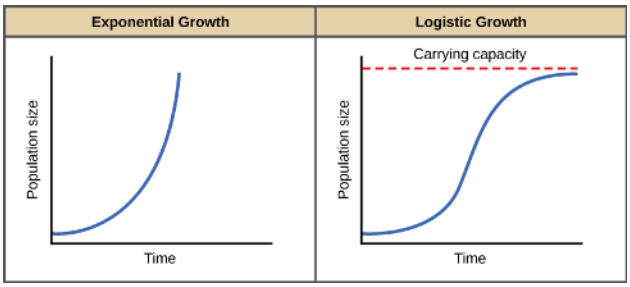


Figure 45.9 When resources are unlimited, populations exhibit exponential growth, resulting in a J-shaped curve. When resources are limited, populations exhibit logistic growth. In logistic growth, population expansion decreases as resources become scarce, and it levels off when the carrying capacity 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 45.9). 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 45.9), 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 45.10a). 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 45.10b). 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.

VISUAL CONNECTION

VISUAL CONNECTION

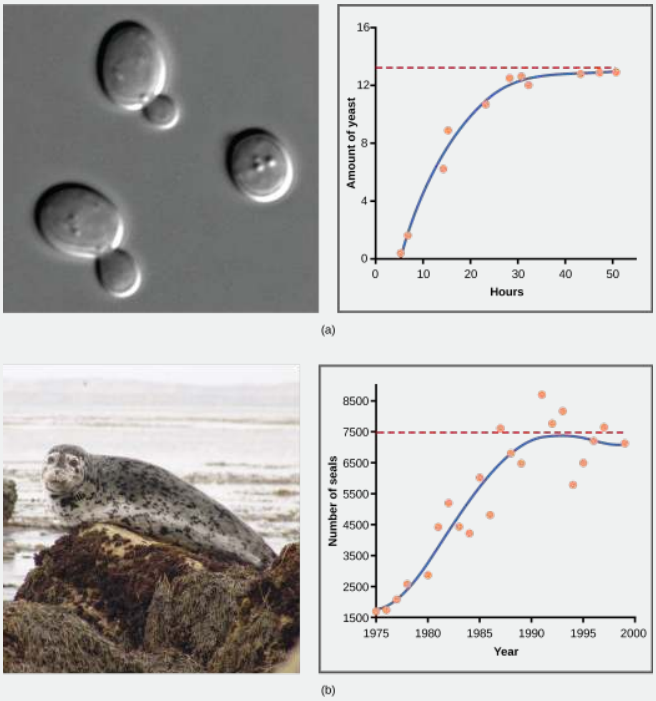


Figure 45.10 (a) Yeast grown in ideal conditions in a test tube show a classical S-shaped logistic growth curve, whereas (b) a natural population of seals shows real-world fluctuation.

If the major food source of the seals declines due to pollution or overfishing, which of the following would likely occur?

1. The carrying capacity of seals would decrease, as would the seal population.
2. The carrying capacity of seals would decrease, but the seal population would remain the same.
3. The number of seal deaths would increase but the number of births would also increase, so the population size would remain the same.
4. The carrying capacity of seals would remain the same, but the population of seals would decrease.

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4.5: POPULATION DYNAMICS AND REGULATION

LEARNING OBJECTIVES

By the end of this section, you will be able to do the following:

- Give examples of how the carrying capacity of a habitat may change
- Compare and contrast density-dependent growth regulation and density-independent growth regulation, giving examples
- Give examples of exponential and logistic growth in wild animal populations
- Describe how natural selection and environmental adaptation leads to the evolution of particular life-history patterns

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 the winter is much lower than it is during the 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 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.

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 45.11 with results from a study focusing on the giant intestinal roundworm (*Ascaris lumbricoides*), a parasite of humans and other mammals.[3] 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.[4] The actual cause of the density-dependence of fecundity in this organism is still unclear and awaiting further investigation.

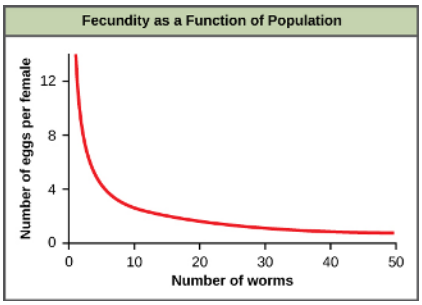


Figure 45.11 In this population of roundworms, fecundity (number of eggs) decreases with population density.[5]

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.

EVOLUTION CONNECTION

EVOLUTION CONNECTION

Why Did the Woolly Mammoth Go Extinct?



Figure 45.12 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)

It's easy to get lost in the discussion about why dinosaurs 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? Scientists are continually exploring these and other theories.

Woolly mammoths began to go extinct much more recently, when they shared the Earth with humans who were no different anatomically than humans today (Figure 45.12). 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. 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 climate change and human hunting led to their extinction. A 2008 study estimated that climate change reduced the mammoth's range from 3,000,000 square miles 42,000 years ago to 310,000 square miles 6,000 years ago.[6] It is also well documented that humans hunted these animals. A 2012 study showed that no single factor was exclusively responsible for the extinction of these magnificent creatures.[7] 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.

LIFE HISTORIES OF *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.

The concept relates to a species' reproductive strategies, 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. Population biologists have grouped species into the two large categories—*K*-selected and *r*-selected—although the categories are really two ends of a continuum.

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 (Table 45.2). 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 45.13a).

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).

In contrast, *r*-selected species have a large number of small offspring (hence their *r* designation (Table 45.2)). 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 45.13b). 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.

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

Table 45.2

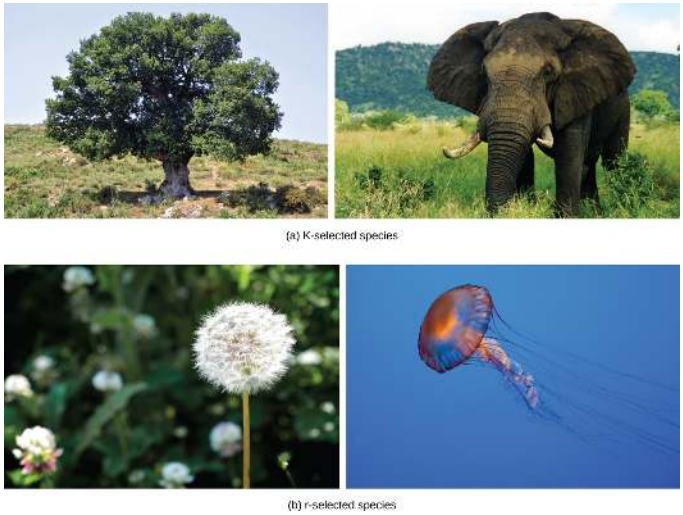


Figure 45.13 (a) Elephants are considered K-selected species as they live long, mature late, and provide long-term parental care to few offspring. Oak trees produce many offspring that do not receive parental care, but are considered K-selected species based on longevity and late maturation. (b) Dandelions and jellyfish are both considered r-selected species as they mature early, have short lifespans, and produce many offspring that receive no parental care.

MODERN THEORIES OF LIFE HISTORY

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 *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 as well as population age structure and mortality factors.

FOOTNOTES

- 3N.A. Croll et al., "The Population Biology and Control of *Ascaris lumbricoides* in a Rural Community in Iran." *Transactions of the Royal Society of Tropical Medicine and Hygiene* 76, no. 2 (1982): 187-197, doi:10.1016/0035-9203(82)90272-3.
- 4Martin Walker et al., "Density-Dependent Effects on the Weight of Female *Ascaris lumbricoides* Infections of Humans and its Impact on Patterns of Egg Production." *Parasites & Vectors* 2, no. 11 (February 2009), doi:10.1186/1756-3305-2-11.
- 5N.A. Croll et al., "The Population Biology and Control of *Ascaris lumbricoides* in a Rural Community in Iran." *Transactions of the Royal Society of Tropical Medicine and Hygiene* 76, no. 2 (1982): 187-197, doi:10.1016/0035-9203(82)90272-3.
- 6David Nogués-Bravo et al., "Climate Change, Humans, and the Extinction of the Woolly Mammoth." *PLoS Biol* 6 (April 2008): e79, doi:10.1371/journal.pbio.0060079.

- 7G.M. MacDonald et al., “Pattern of Extinction of the Woolly Mammoth in Beringia.” *Nature Communications* 3, no. 893 (June 2012), doi:10.1038/ncomms1881.

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4.6: HUMAN POPULATION GROWTH

LEARNING OBJECTIVES

By the end of this section, you will be able to do the following:

- Discuss exponential human population growth
- 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

Population dynamics can be applied to human population growth. 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. 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. 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 world's carrying capacity for human beings might actually decrease.

The human population is currently experiencing exponential growth even though human reproduction is far below its biotic potential (Figure 45.14). 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.

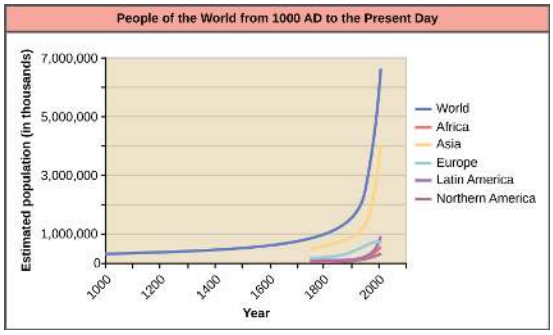


Figure 45.14 Human population growth since 1000 AD is exponential (dark blue line). Notice that while the population in Asia (yellow line), which has many economically underdeveloped countries, is increasing exponentially, the population in Europe (light blue line), where most of the countries are economically developed, is growing much more slowly.

A consequence of exponential human population growth is a reduction in time that it takes to add a particular number of humans to the Earth. Figure 45.15 shows that 123 years were necessary to add 1 billion humans in 1930, but it only took 24 years to add two billion people between 1975 and 1999. As already discussed, our ability to increase our carrying capacity indefinitely may be limited. 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.

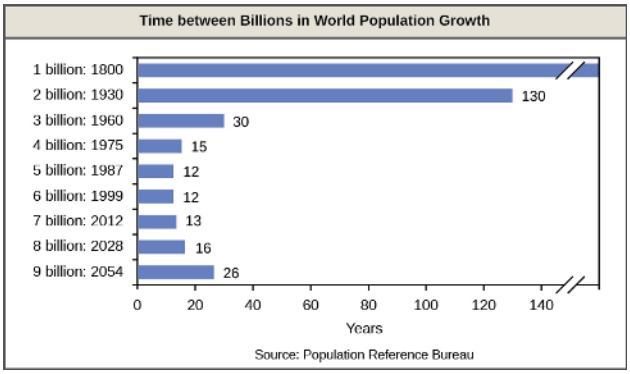


Figure 45.15 The time between the addition of each billion human beings to Earth decreases over time. (credit: modification of work by Ryan T. Cragun)

LINK TO LEARNING

LINK TO LEARNING

Click through this video of how human populations have changed over time.

OVERCOMING DENSITY-DEPENDENT REGULATION

Humans are unique in their ability to alter their environment with the conscious purpose of increasing 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, and communication. Humans can construct shelter 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 the 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 plaque 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 Institute for Health Metrics and Evaluation (IHME) in Seattle, global death from infectious disease declined from 15.4 million in 1990 to 10.4 million in 2017. To compare 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 0.14 percent. Thus, infectious disease influence on human population growth is becoming less significant.

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 45.16). This pattern is most often observed in underdeveloped countries where individuals do not live to old age because of less-than-optimal living conditions. Age structures of areas with slow growth, including developed countries such as the United States, still have a pyramidal structure, but with many fewer young and reproductive-aged individuals and a greater proportion of older individuals. Other developed countries, such as Italy, have zero population growth. The age structure of these populations is more conical, with an even greater percentage of middle-aged and older individuals. The actual growth rates in different countries are shown in Figure 45.17, with the highest rates tending to be in the less economically developed countries of Africa and Asia.

VISUAL CONNECTION

VISUAL CONNECTION

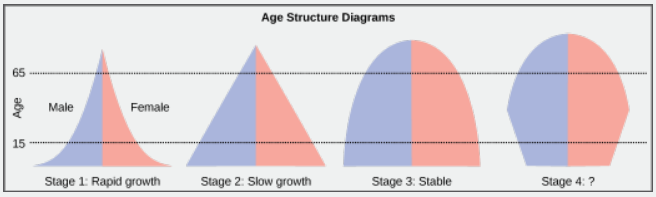


Figure 45.16 Typical age structure diagrams are shown. The rapid growth diagram narrows to a point, indicating that the number of individuals decreases rapidly with age. In the slow growth model, the number of individuals decreases steadily with age. Stable population diagrams are rounded on the top, showing that the number of individuals per age group decreases gradually, and then increases for the older part of the population.

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?

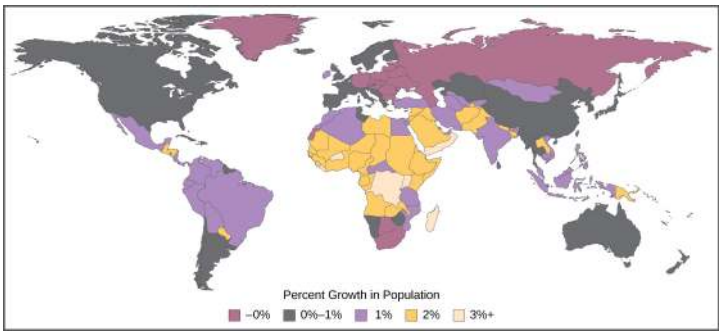


Figure 45.17 The percent growth rate of population in different countries is shown. Notice that the highest growth is occurring in less economically developed countries in Africa and Asia.

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."[8] While many experts view this statement as incorrect based on evidence, the laws of exponential population growth are still in effect, and unchecked human population growth cannot continue indefinitely.

Several nations have instituted policies aimed at influencing population. Efforts to control population growth led to the one-child policy in China, which is now being phased out. India also implements national and regional policies to encourage family planning. On the other hand, Japan, Spain, Russia, Iran, and other countries have made efforts to increase population growth after birth rates dipped. Such policies are controversial, and the human population continues to grow. At some point the food supply may run out, but the outcomes are difficult to predict. The United Nations estimates that future world population growth may vary from 6 billion (a decrease) to 16 billion people by the year 2100.

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 emission of the greenhouse gas carbon dioxide. However, these treaties have not been ratified by every country. The role of human activity in causing climate change has become a hotly debated socio-political issue in some countries, including the United States. Thus, we enter the future with considerable uncertainty about our ability to curb human population growth and protect our environment.

LINK TO LEARNING

LINK TO LEARNING

Visit this website and select "Launch movie" for an animation discussing the global impacts of human population growth.

FOOTNOTES

- 8Paul R. Erlich, prologue to *The Population Bomb*, (1968; repr., New York: Ballantine, 1970).

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4.7: KEY TERMS

age structure
proportion of population members at specific age ranges

aggressive display
visual display by a species member to discourage other members of the same species or different species

aposematic coloration
warning coloration used as a defensive mechanism against predation

Batesian mimicry
type of mimicry where a non-harmful species takes on the warning colorations of a harmful one

behavior
change in an organism's activities in response to a stimulus

behavioral biology
study of the biology and evolution of behavior

biotic potential (r_{max})
maximal potential growth rate of a species

birth rate (*B*)
number of births within a population at a specific point in time

camouflage
avoid detection by blending in with the background

carrying capacity (*K*)
number of individuals of a species that can be supported by the limited resources of a habitat

classical conditioning
association of a specific stimulus and response through conditioning

climax community
final stage of succession, where a stable community is formed by a characteristic assortment of plant and animal species

cognitive learning
knowledge and skills acquired by the manipulation of information in the mind

commensalism
relationship between species wherein one species benefits from the close, prolonged interaction, while the other species neither benefits nor is harmed

competitive exclusion principle
no two species within a habitat can coexist when they compete for the same resources at the same place and time

conditioned behavior
behavior that becomes associated with a specific stimulus through conditioning

courtship display
visual display used to attract a mate

death rate (*D*)
number of deaths within a population at a specific point in time

demographic-based population model
modern model of population dynamics incorporating many features of the *r*- and *K*-selection theory

demography
statistical study of changes in populations over time

density-dependent regulation
regulation of population that is influenced by population density, such as crowding effects; usually involves biotic factors

density-independent regulation
regulation of populations by factors that operate independent of population density, such as forest fires and volcanic eruptions; usually involves abiotic factors

distraction display
visual display used to distract predators away from a nesting site

Emsleyan/Mertensian mimicry
type of mimicry where a harmful species resembles a less harmful one

energy budget
allocation of energy resources for body maintenance, reproduction, and parental care

environmental disturbance
change in the environment caused by natural disasters or human activities

ethology
biological study of animal behavior

exponential growth
accelerating growth pattern seen in species under conditions where resources are not limiting

fecundity
potential reproductive capacity of an individual

fixed action pattern
series of instinctual behaviors that, once initiated, always goes to completion regardless of changes in the environment

foraging
behaviors species use to find food

foundation species
species which often forms the major structural portion of the habitat

habituation
ability of a species to ignore repeated stimuli that have no consequence

host
organism a parasite lives on

imprinting
identification of parents by newborns as the first organism they see after birth

innate behavior
instinctual behavior that is not altered by changes in the environment

intersexual selection
selection of a desirable mate of the opposite sex

interspecific competition

competition between species for resources in a shared habitat or environment

intrasexual selection
competition between members of the same sex for a mate

intraspecific competition
competition between members of the same species

island biogeography
study of life on island chains and how their geography interacts with the diversity of species found there

iteroparity
life history strategy characterized by multiple reproductive events during the lifetime of a species

J-shaped growth curve
shape of an exponential growth curve

***K*-selected species**
species suited to stable environments that produce a few, relatively large offspring and provide parental care

keystone species
species whose presence is key to maintaining biodiversity in an ecosystem and to upholding an ecological community's structure

kin selection
sacrificing one's own life so that one's genes will be passed on to future generations by relatives

kinesis
undirected movement of an organism in response to a stimulus

learned behavior
behavior that responds to changes in the environment

life history
inherited pattern of resource allocation under the influence of natural selection and other evolutionary forces

life table
table showing the life expectancy of a population member based on its age

logistic growth
leveling off of exponential growth due to limiting resources

mark and recapture
technique used to determine population size in mobile organisms

migration
long-range seasonal movement of animal species

monogamy
mating system whereby one male and one female remain coupled for at least one mating season

mortality rate
proportion of population surviving to the beginning of an age interval that die during the age interval

Müllerian mimicry
type of mimicry where species share warning coloration and all are harmful to predators

mutualism
symbiotic relationship between two species where both species benefit

one-child policy
China's policy to limit population growth by limiting urban couples to have only one child or face the penalty of a fine

operant conditioning
learned behaviors in response to positive and/or negative reinforcement

parasite
organism that uses resources from another species, the host

pioneer species
first species to appear in primary and secondary succession

polyandry
mating system where one female mates with many males

polygyny
mating system where one male mates with many females

population density
number of population members divided by the area or volume being measured

population growth rate
number of organisms added in each reproductive generation

population size (*N*)
number of population members in a habitat at the same time

primary succession
succession on land that previously has had no life

quadrat
square made of various materials used to determine population size and density in slow moving or stationary organisms

***r*-selected species**
species suited to changing environments that produce many offspring and provide little or no parental care

reflex action
action in response to direct physical stimulation of a nerve

relative species abundance
absolute population size of a particular species relative to the population sizes of other species within the community

S-shaped growth curve
shape of a logistic growth curve

secondary succession
succession in response to environmental disturbances that move a community away from its equilibrium

semelparity
life history strategy characterized by a single reproductive event followed by death

signal
method of communication between animals including those obtained by the senses of smell, hearing, sight, or touch

species dispersion pattern
(also, species distribution pattern) spatial location of individuals of a given species within a habitat at a particular point in time

species richness

number of different species in a community

survivorship curve

graph of the number of surviving population members versus the relative age of the member

symbiosis

close interaction between individuals of different species over an extended period of time that impacts the abundance and distribution of the associating populations

taxis

directed movement in response to a stimulus

zero population growth

steady population size where birth rates and death rates are equal

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4.8: CHAPTER SUMMARY

45.1 POPULATION DEMOGRAPHY

Populations are individuals of a species that live in a particular habitat. Ecologists measure characteristics of populations: size, density, dispersion pattern, age structure, and sex ratio. Life tables are useful to calculate life expectancies of individual population members. Survivorship curves show the number of individuals surviving at each age interval plotted versus time.

45.2 LIFE HISTORIES AND NATURAL SELECTION

All species have evolved a pattern of living, called a life history strategy, in which they partition energy for growth, maintenance, and reproduction. These patterns evolve through natural selection; they allow species to adapt to their environment to obtain the resources they need to successfully reproduce. There is an inverse relationship between fecundity and parental care. A species may reproduce early in life to ensure surviving to a reproductive age or reproduce later in life to become larger and healthier and better able to give parental care. A species may reproduce once (semelparity) or many times (iteroparity) in its life.

45.3 ENVIRONMENTAL LIMITS TO POPULATION GROWTH

Populations with unlimited resources grow exponentially, with an accelerating growth rate. When resources become limiting, populations follow a logistic growth curve. The population of a species will level off at the carrying capacity of its environment.

45.4 POPULATION DYNAMICS AND REGULATION

Populations are regulated by a variety of density-dependent and density-independent factors. Species are divided into two categories based on a variety of features of their life history patterns: *r*-selected species, which have large numbers of offspring, and *K*-selected species, which have few offspring. The *r*- and *K*-selection theory has fallen out of use; however, many of its key features are still used in newer, demographically-based models of population dynamics.

45.5 HUMAN POPULATION GROWTH

The world's human population is growing at an exponential rate. Humans have increased the world's carrying capacity through migration, agriculture, medical advances, and communication. The age structure of a population allows us to predict population growth. Unchecked human population growth could have dire long-term effects on our environment.

45.6 COMMUNITY ECOLOGY

Communities include all the different species living in a given area. The variety of these species is called species richness. Many organisms have developed defenses against predation and herbivory, including mechanical defenses, warning coloration, and mimicry, as a result of evolution and the interaction with other members of the community. Two species cannot exist in the same habitat competing directly for the same resources. Species may form symbiotic relationships such as commensalism or mutualism. Community structure is described by its foundation and keystone species. Communities respond to environmental disturbances by succession (the predictable appearance of different types of plant species) until a stable community structure is established.

45.7 BEHAVIORAL BIOLOGY: PROXIMATE AND ULTIMATE CAUSES OF BEHAVIOR

Behaviors are responses to stimuli. They can either be instinctual/innate behaviors, which are not influenced by the environment, or learned behaviors, which are influenced by environmental changes. Instinctual behaviors include mating systems and methods of communication. Learned behaviors include imprinting and habituation, conditioning, and, most powerfully, cognitive learning.

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4.9: VISUAL CONNECTION QUESTIONS

1.

Figure 45.2 As this graph shows, population density typically decreases with increasing body size. Why do you think this is the case?

2.

Figure 45.10b If the major food source of the seals declines due to pollution or overfishing, which of the following would likely occur?

1. The carrying capacity of seals would decrease, as would the seal population.
2. The carrying capacity of seals would decrease, but the seal population would remain the same.
3. The number of seal deaths would increase but the number of births would also increase, so the population size would remain the same.
4. The carrying capacity of seals would remain the same, but the population of seals would decrease.

3.

Figure 45.16 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?

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4.10: REVIEW QUESTIONS

4.

Which of the following methods will tell an ecologist about both the size and density of a population?

1. mark and recapture
2. mark and release
3. quadrat
4. life table

5.

Which of the following is best at showing the life expectancy of an individual within a population?

1. quadrat
2. mark and recapture
3. survivorship curve
4. life table

6.

Humans have which type of survivorship curve?

1. Type I
2. Type II
3. Type III
4. Type IV

7.

How is a clumped population distribution beneficial for prey animals?

1. Being a member of a larger group provides protection for each individual from predators.
2. Prey animals rely on each other to acquire food.
3. Prey animals live in small family groups to raise young.
4. Clumped population distributions ensure that at least one member of the population knows how to identify the seasonal migration route.

8.

Which of the following is associated with long-term parental care?

1. few offspring
2. many offspring
3. semelparity
4. fecundity

9.

Which of the following is associated with multiple reproductive episodes during a species' lifetime?

1. semiparity
2. iteroparity
3. semelparity
4. fecundity

10.

Which of the following is associated with the reproductive potential of a species?

1. few offspring
2. many offspring
3. semelparity
4. fecundity

11.

Species with limited resources usually exhibit a(n) _____ growth curve.

1. logistic
2. logical

3. experimental
4. exponential

12.

The maximum rate of increased characteristic of a species is called its _____.

1. limit
2. carrying capacity
3. biotic potential
4. exponential growth pattern

13.

The population size of a species capable of being supported by the environment is called its _____.

1. limit
2. carrying capacity
3. biotic potential
4. logistic growth pattern

14.

Species that have many offspring at one time are usually:

1. *r*-selected
2. *K*-selected
3. both *r*- and *K*-selected
4. not selected

15.

A forest fire is an example of _____ regulation.

1. density-dependent
2. density-independent
3. *r*-selected
4. *K*-selected

16.

Primates are examples of:

1. density-dependent species
2. density-independent species
3. *r*-selected species
4. *K*-selected species

17.

Which of the following statements does not support the conclusion that giraffes are *k*-selected species?

1. Giraffes are approximately 6’ tall and weigh 150 lbs at birth.
2. Wild giraffes begin mating at 6-7 years of age.
3. Newborn giraffes are capable of coordinated walking within an hour of birth, and running within 24 hours of birth.
4. Giraffes rarely give birth to twins.

18.

Which of the following events would **not** negatively impact Yellowstone’s grey wolf carrying capacity?

1. snow in winter
2. a beaver damming a river upstream
3. a forest fire
4. chronic wasting disease in the deer population

19.

A country with zero population growth is likely to be _____.

1. in Africa
2. in Asia

3. economically developed
4. economically underdeveloped

20.

Which type of country has the greatest proportion of young individuals?

1. economically developed
2. economically underdeveloped
3. countries with zero population growth
4. countries in Europe

21.

Which of the following is not a way that humans have increased the carrying capacity of the environment?

1. agriculture
2. using large amounts of natural resources
3. domestication of animals
4. use of language

22.

The first species to live on new land, such as that formed from volcanic lava, are called _____.

1. climax community
2. keystone species
3. foundation species
4. pioneer species

23.

Which type of mimicry involves multiple species with similar warning coloration that are all toxic to predators?

1. Batesian mimicry
2. Müllerian mimicry
3. Emsleyan/Mertensian mimicry
4. Mertensian mimicry

24.

A symbiotic relationship where both of the coexisting species benefit from the interaction is called _____.

1. commensalism
2. parasitism
3. mutualism
4. communism

25.

Which of the following is **not** a mutualistic relationship?

1. a shark using an aquatic cleaning station
2. a helminth feeding from its host
3. a bumblebee collecting pollen from a flower
4. bacteria living in the gut of humans

26.

The ability of rats to learn how to run a maze is an example of _____.

1. imprinting
2. classical conditioning
3. operant conditioning
4. cognitive learning

27.

The training of animals usually involves _____.

1. imprinting
2. classical conditioning

3. operant conditioning
4. cognitive learning

28.

The sacrifice of the life of an individual so that the genes of relatives may be passed on is called _____.

1. operant learning
2. kin selection
3. kinesis
4. imprinting

29.

Why are polyandrous mating systems more rare than polygynous matings?

1. Only males are capable of multiple rounds of reproduction within a single breeding season.
2. Only females care for the young.
3. Females usually experience more intrasexual selection pressure than males.
4. Females usually devote more energy to offspring production and development.

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4.11: CRITICAL THINKING QUESTIONS

30.

Describe how a researcher would determine the size of a penguin population in Antarctica using the mark and release method.

31.

The CDC released the following data in its 2013 Vital Statistics report.

Age interval	Number dying in age interval	Number surviving at beginning of age interval
0-10	756	100,000
11-20	292	99,244
21-30	890	98,953
31-40	1,234	98,164
41-50	2,457	96,811
51-60	5,564	94,352
61-70	10,479	88,788

Table 45.3

Calculate the mortality rate for each age interval, and describe the trends in adult and childhood mortality per 100,000 births in the United States in 2013.

32.

Why is long-term parental care not associated with having many offspring during a reproductive episode?

33.

Describe the difference in evolutionary pressures experienced by an animal that begins reproducing early and an animal that reproduces late in its lifecycle.

34.

Describe the rate of population growth that would be expected at various parts of the S-shaped curve of logistic growth.

35.

Describe how the population of a species that survives a mass extinction event would change in size and growth pattern over time beginning immediately after the extinction event.

36.

Give an example of how density-dependent and density-independent factors might interact.

37.

Describe the age structures in rapidly growing countries, slowly growing countries, and countries with zero population growth.

38.

Since the introduction of the Endangered Species Act the number of species on the protected list has more than doubled. Describe how the human population’s growth pattern contributes to the rise in endangered species.

39.

Describe the competitive exclusion principle and its effects on competing species.

40.

Jaguars are a keystone species in the Amazon. Describe how they can be so essential to the ecosystem despite being significantly less abundant than many other species.

41.

Describe Pavlov’s dog experiments as an example of classical conditioning.

42.

Describe the advantage of using an aural or pheromone signal to attract a mate as opposed to a visual signal. How might the population density contribute to the evolution of aural or visual mating rituals?

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CHAPTER OVERVIEW

5: COMMUNITY ECOLOGY

5.1: Community Ecology Concepts

5.2: Biological Communities

5.3: Community Succession and Stability

5.4: Invasive Species Ecology

5.5: Species Richness and Diversity

5.6: Island Biogeography and Habitat Fragmentation

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5.1: COMMUNITY ECOLOGY CONCEPTS

LEARNING OBJECTIVES

By the end of this section, you will be able to do the following:

- Discuss the predator-prey cycle
- Give examples of defenses against predation and herbivory
- Describe the competitive exclusion principle
- Give examples of symbiotic relationships between species
- Describe community structure and succession

Populations rarely, if ever, live in isolation from populations of other species. In most cases, numerous species share a habitat. The interactions between these populations play a major role in regulating population growth and abundance. All populations occupying the same habitat form a community: populations 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.

PREDATION AND HERBIVORY

Perhaps the classical example of species interaction is predation: the consumption of prey by its predator. Nature shows on television highlight the drama of one living organism killing another. Populations of predators and prey in a community are not constant over time: in most cases, they vary in cycles that appear to be related. The most often cited example of predator-prey dynamics is seen in the cycling of the lynx (predator) and the snowshoe hare (prey), using nearly 200 year-old trapping data from North American forests (Figure 45.18). This cycle of predator and prey lasts approximately 10 years, with the predator population lagging 1–2 years behind that of the prey population. As the hare numbers increase, there is more food available for the lynx, allowing the lynx population to increase as well. When the lynx population grows to a threshold level, however, they kill so many hares that hare population begins to decline, followed by a decline in the lynx population because of scarcity of food. When the lynx population is low, the hare population size begins to increase due, at least in part, to low predation pressure, starting the cycle anew.

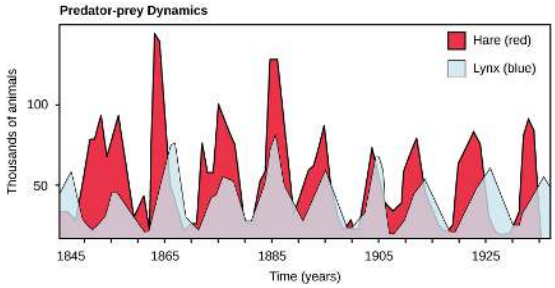


Figure 45.18 The cycling of lynx and snowshoe hare populations in Northern Ontario is an example of predator-prey dynamics.

Some researchers question the idea that predation models entirely control the population cycling of the two species. More recent studies have pointed to undefined density-dependent factors as being important in the cycling, in addition to predation. One possibility is that the cycling is inherent in the hare population due to density-dependent effects such as lower fecundity (maternal stress) caused by crowding when the hare population gets too dense. The hare cycling would then induce the cycling of the lynx because it is the lynxes' major food source. The more we study communities, the more complexities we find, allowing ecologists to derive more accurate and sophisticated models of population dynamics.

Herbivory describes the consumption of plants by insects and other animals, and it is another interspecific relationship that affects populations. Unlike animals, most plants cannot outrun predators or use mimicry to hide from hungry animals. Some plants have developed mechanisms to defend against herbivory. Other species have developed mutualistic relationships; for example, herbivory provides a mechanism of seed distribution that aids in plant reproduction.

DEFENSE MECHANISMS AGAINST PREDATION AND HERBIVORY

The study of communities must consider evolutionary forces that act on the members of the various populations contained within it. Species are not static, but slowly changing and adapting to their environment by natural selection and other evolutionary forces. Species have evolved numerous mechanisms to escape predation and herbivory. These defenses may be mechanical, chemical, physical, or behavioral.

Mechanical defenses, such as the presence of thorns on plants or the hard shell on turtles, discourage animal predation and herbivory by causing physical pain to the predator or by physically preventing the predator from being able to eat the prey. Chemical defenses are produced by many animals as well as plants, such as the foxglove which is extremely toxic when eaten. Figure 45.19 shows some organisms' defenses against predation and herbivory.

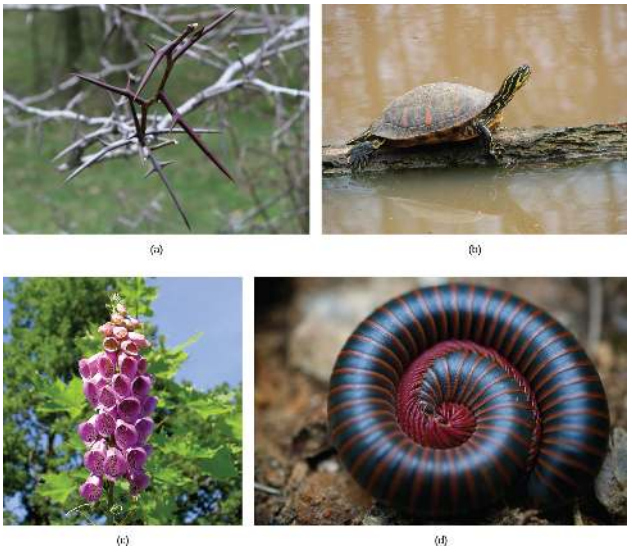


Figure 45.19 The (a) honey locust tree (*Gleditsia triacanthos*) uses thorns, a mechanical defense, against herbivores, while the (b) Florida red-bellied turtle (*Pseudemys nelsoni)* uses its shell as a mechanical defense against predators. (c) Foxglove (*Digitalis* sp.) uses a chemical defense: toxins produced by the plant can cause nausea, vomiting, hallucinations, convulsions, or death when consumed. (d) The North American millipede (*Narceus americanus*) uses both mechanical and chemical defenses: when threatened, the millipede curls into a defensive ball and produces a noxious substance that irritates eyes and skin. (credit a: modification of work by Huw Williams; credit b: modification of work by "JamieS93"/Flickr; credit c: modification of work by Philip Jägenstedt; credit d: modification of work by Cory Zanker)

Many species use physical appearance, such as body shape and coloration, to avoid being detected by predators. The tropical walking stick is an insect with the coloration and body shape of a twig which makes it very hard to see when stationary against a background of real twigs (Figure 45.20a). In another example, the chameleon can, within limitations, change its color to match its surroundings (Figure 45.20b). Both of these are examples of camouflage, or avoiding detection by blending in with the background. There are many behavioral adaptations to avoid or confuse predators. Playing dead and traveling in large groups, like schools of fish or flocks of birds, are both behaviors that reduce the risk of being eaten.



(a) (b)

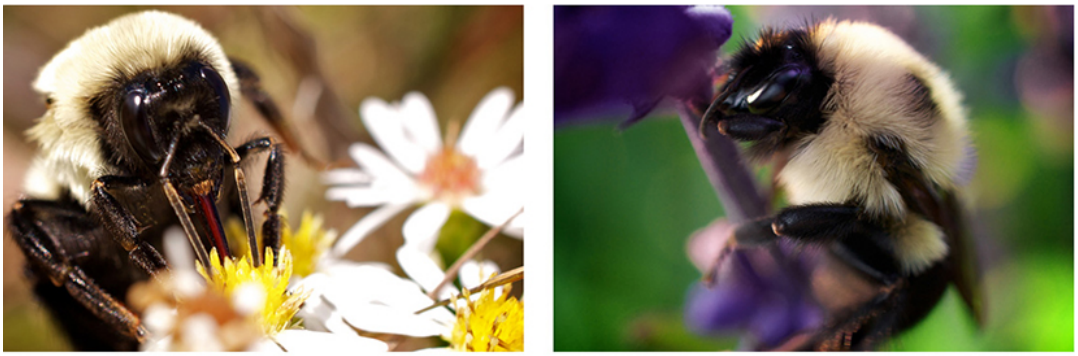
Figure 45.20 (a) The tropical walking stick and (b) the chameleon use body shape and/or coloration to prevent detection by predators. (credit a: modification of work by Linda Tanner; credit b: modification of work by Frank Vassen)

Some species use coloration as a way of warning predators that they are not good to eat. For example, the cinnabar moth caterpillar, the fire-bellied toad, and many species of beetle have bright colors that warn of a foul taste, the presence of toxic chemicals, and/or the ability to sting or bite, respectively. Predators that ignore this coloration and eat the organisms will experience their unpleasant taste or presence of toxic chemicals and learn not to eat them in the future. This type of defensive mechanism is called aposematic coloration, or warning coloration (Figure 45.21).



Figure 45.21 (a) The strawberry poison dart frog (*Oophaga pumilio*) uses aposematic coloration to warn predators that it is toxic, while the (b) striped skunk (*Mephitis mephitis*) uses aposematic coloration to warn predators of the unpleasant odor it produces. (credit a: modification of work by Jay Iwasaki; credit b: modification of work by Dan Dzurisin)

While some predators learn to avoid eating certain potential prey because of their coloration, other species have evolved mechanisms to mimic this coloration to avoid being eaten, even though they themselves may not be unpleasant to eat or contain toxic chemicals. In Batesian mimicry, a harmless species imitates the warning coloration of a harmful one. Assuming they share the same predators, this coloration then protects the harmless ones, even though they do not have the same level of physical or chemical defenses against predation as the organism they mimic. Many insect species mimic the coloration of wasps or bees, which are stinging, venomous insects, thereby discouraging predation (Figure 45.22).



(a) (b)

Figure 45.22 Batesian mimicry occurs when a harmless species mimics the coloration of a harmful species, as is seen with the (a) bumblebee and (b) bee-like robber fly. (credit a, b: modification of work by Cory Zanker)

In Müllerian mimicry, multiple species share the same warning coloration, but all of them actually have defenses. Figure 45.23 shows a variety of foul-tasting butterflies with similar coloration. In Emsleyan/Mertensian mimicry, a deadly prey mimics a less dangerous one, such as the venomous coral snake mimicking the nonvenomous milk snake. This type of mimicry is extremely rare and more difficult to understand than the previous two types. For this type of mimicry to work, it is essential that eating the milk snake has unpleasant but not fatal consequences. Then, these predators learn not to eat snakes with this coloration, protecting the coral snake as well. If the snake were fatal to the predator, there would be no opportunity for the predator to learn not to eat it, and the benefit for the less toxic species would disappear.



Figure 45.23 Several unpleasant-tasting *Heliconius* butterfly species share a similar color pattern with better-tasting varieties, an example of Müllerian mimicry. (credit: Joron M, Papa R, Beltrán M, Chamberlain N, Mavárez J, et al.)

LINK TO LEARNING

LINK TO LEARNING

Go to this website to view stunning examples of mimicry.

COMPETITIVE EXCLUSION PRINCIPLE

Resources are often limited within a habitat and multiple species may compete to obtain them. All species have an ecological niche in the ecosystem, which describes how they acquire the resources they need and how they interact with other species in the community. The competitive exclusion principle states that two species cannot occupy the same niche in a habitat. In other words, different species cannot coexist in a community if they are competing for all the same resources. An example of this principle is shown in Figure 45.24, with two protozoan species, *Paramecium aurelia* and *Paramecium caudatum*. When grown individually in the laboratory, they both thrive. But when they are placed together in the same test tube (habitat), *P. aurelia* outcompetes *P. caudatum* for food, leading to the latter's eventual extinction.

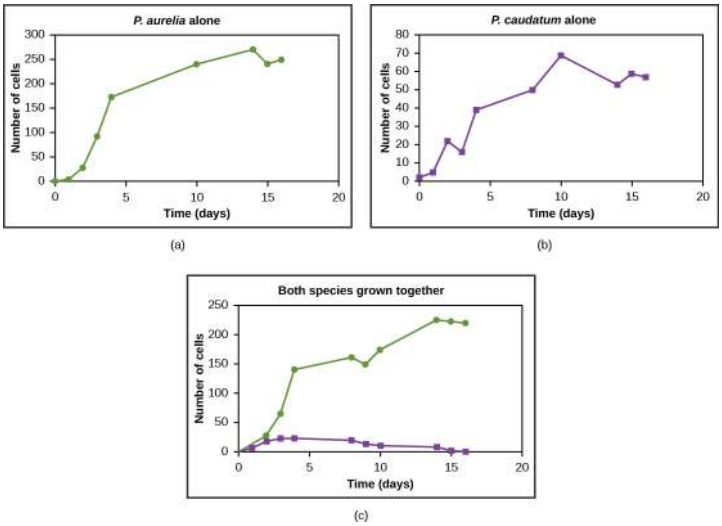


Figure 45.24 *Paramecium aurelia* and *Paramecium caudatum* grow well individually, but when they compete for the same resources, the *P. aurelia* outcompetes the *P. caudatum*.

This exclusion may be avoided if a population evolves to make use of a different resource, a different area of the habitat, or feeds during a different time of day, called resource partitioning. The two organisms are then said to occupy different microniches. These organisms coexist by minimizing direct competition.

SYMBIOSIS

Symbiotic relationships, or symbioses (plural), are close interactions between individuals of different species over an extended period of time which impact the abundance and distribution of the associating populations. Most scientists accept this definition, but some restrict the term to only those species that are mutualistic, where both individuals benefit from the interaction. In this discussion, the broader definition will be used.

COMMENSALISM

A commensal relationship occurs when one species benefits from the close, prolonged interaction, while the other neither benefits nor is harmed. Birds nesting in trees provide an example of a commensal relationship (Figure 45.25). 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. Another example of a commensal relationship is the pilot fish and the shark. The pilot fish feed on the leftovers of the host's meals, and the host is not affected in any way.



Figure 45.25 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)

MUTUALISM

A second type of symbiotic relationship is called mutualism, where two species benefit from their interaction. Some scientists believe that these are the only true examples of symbiosis. For example, termites have a mutualistic relationship with protozoa that live in the insect's gut (Figure 45.26a). The termite benefits from the ability of bacterial symbionts within the protozoa to digest cellulose. The termite itself cannot do this, and without the protozoa, it would not be able to obtain energy from its food (cellulose from the wood it chews and eats). The protozoa and the bacterial symbionts benefit by having a protective environment and a constant supply of food from the wood chewing actions of the termite. Lichens have a mutualistic relationship between fungus and photosynthetic algae or bacteria (Figure 45.26b). As these symbionts grow together, 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.



(a) (b)

Figure 45.26 (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)

PARASITISM

A parasite is an organism that lives in or on another living organism and derives nutrients from it. In this relationship, the parasite benefits, but the host is harmed. The host is usually weakened by the parasite as it siphons resources the host would normally use to maintain itself. The parasite, however, is unlikely to kill the host, especially not quickly, because this would allow no time for the organism to complete its reproductive cycle by spreading to another host.

The reproductive cycles of parasites are often very complex, sometimes requiring more than one host species. A tapeworm is a parasite that causes disease in humans when contaminated, undercooked meat is consumed (Figure 45.27). The tapeworm can live inside the intestine of the host for several years, benefiting from the food the host is eating, and may grow to be over 50 ft long by adding segments. The parasite moves from species to species in a cycle, making two hosts necessary to complete its life cycle.

Another common parasite is *Plasmodium falciparum*, the protozoan cause of malaria, a significant disease in many parts of the world. Living in human liver and red blood cells, the organism reproduces asexually in the gut of blood-feeding mosquitoes to complete its life cycle. Thus malaria is spread from human to human by mosquitoes, one of many arthropod-borne infectious diseases.

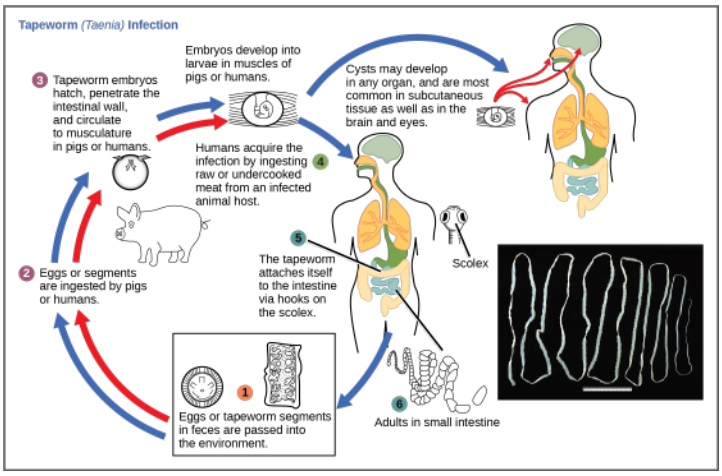


Figure 45.27 This diagram shows the life cycle of a pork tapeworm (*Taenia solium*), a human worm parasite. (credit: modification of work by CDC)

CHARACTERISTICS OF COMMUNITIES

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, or 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 (Figure 45.28). 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 45.28 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 by the number of different species (species richness) in a particular area and their relative abundance (species evenness). The area in question could be a habitat, a biome, or the entire biosphere. Species richness is the term that is used to describe the number of species living in a habitat or biome. Species richness varies across the globe (Figure 45.29). 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. Relative species abundance is the number of individuals in a species relative to the total number of individuals in all species within a habitat, ecosystem, or biome. Foundation species often have the highest relative abundance of species.

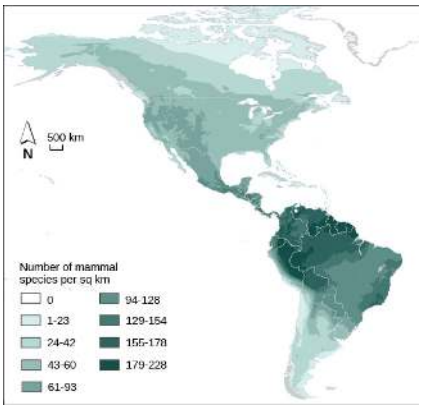


Figure 45.29 The greatest species richness for mammals in North and South America is associated with the equatorial latitudes. (credit: modification of work by NASA, CIESIN, Columbia University)

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 (Figure 45.30). 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 45.30 The *Pisaster ochraceus* sea star is a keystone species. (credit: Jerry Kirkhart)

EVERYDAY CONNECTION

EVERYDAY CONNECTION

Invasive SpeciesInvasive species are nonnative 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 45.31. Whether enjoying a forest hike, taking a summer boat trip, or simply walking down an urban street, you have likely encountered an invasive species.

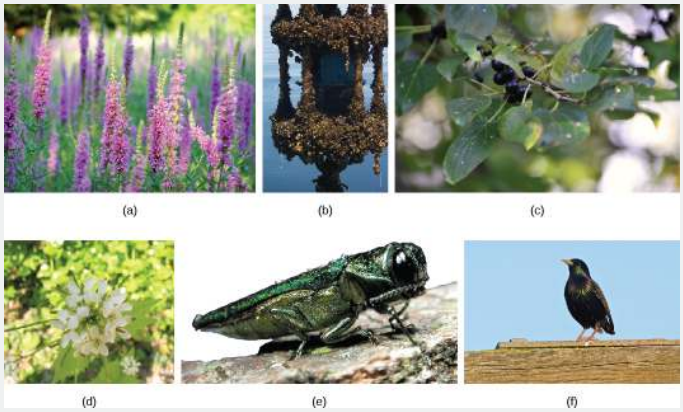


Figure 45.31 In the United States, invasive species like (a) purple loosestrife (*Lythrum salicaria*) and the (b) zebra mussel (*Dreissena polymorpha*) threaten certain aquatic ecosystems. Some forests are threatened by the spread of (c) common buckthorn (*Rhamnus cathartica*), (d) garlic mustard (*Alliaria 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).

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.

PRIMARY SUCCESSION AND PIONEER SPECIES

Primary succession occurs when new land is formed or rock is exposed: for example, following the eruption of volcanoes, such as those on the Big Island of Hawaii. As lava flows into the ocean, new land is continually being formed. On the Big Island, approximately 32 acres of land is added each year. First, weathering and other natural forces break down the substrate enough for the establishment of certain hearty plants and lichens with few soil requirements, known as pioneer species (Figure 45.32). These species help to further break down the mineral rich lava into soil where other, less hardy species will grow and eventually replace the pioneer species. In addition, as these early species grow and die, they add to an ever-growing layer of decomposing organic material and contribute to soil formation. Over time the area will reach an equilibrium state, with a set of organisms quite different from the pioneer species.



Figure 45.32 During primary succession in lava on Maui, Hawaii, succulent plants are the pioneer species. (credit: Forest and Kim Starr)

SECONDARY SUCCESSION

A classic example of secondary succession occurs in oak and hickory forests cleared by wildfire (Figure 45.33). Wildfires will burn most vegetation and kill those animals unable to flee the area. Their nutrients, however, are returned to the ground in the form of ash. Thus, even when areas are devoid of life due to severe fires, the area will soon be ready for new life to take hold.

Before the fire, the vegetation was dominated by tall trees with access to the major plant energy resource: sunlight. Their height gave them access to sunlight while also shading the ground and other low-lying species. After the fire, though, these trees are no longer dominant. Thus, the first plants to grow back are usually annual plants followed within a few years by quickly growing and spreading grasses and other pioneer species. Due to, at least in part, changes in the environment brought on by the growth of the grasses and other species, over many years, shrubs will emerge along with small pine, oak, and hickory trees. These organisms are called intermediate species. Eventually, over 150 years, the forest will reach its equilibrium point where species composition is no longer changing and resembles the community before the fire. This equilibrium state is referred to as the climax community, which will remain stable until the next disturbance.

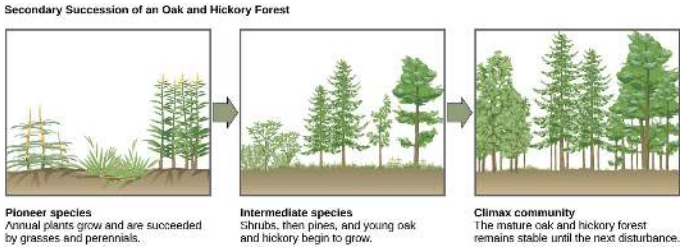


Figure 45.33 Secondary succession is shown in an oak and hickory forest after a forest fire.

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SECTION OVERVIEW

5.2: Biological Communities

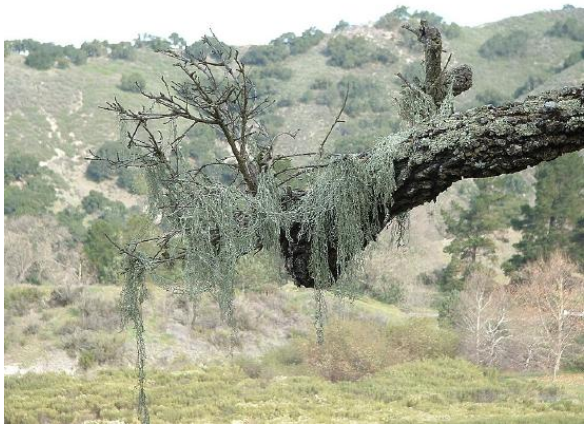
A ***community*** or ***biocoenosis*** is *an assemblage of organisms (species populations) whose composition and aspect is determined by the properties of the environment and by the relations of the organisms to each other* (modified from Braatne, 2005). Möbius proposed the term *biocoenosis* in 1877 in his study of oyster reefs in the North Sea, recognizing that interactions between species in a structurally complex system brought with it a higher level of functional complexity. Shelford defined a community as an "assemblage with unity of taxonomic composition and a relatively uniform appearance (Odum, 1959)." The *biotic community*, along with the physical or abiotic elements of the environment together constitute the ***ecosystem***- how a community of organisms interact with their environment of Tansley (1935).

Like an "ecosystem," the size or area occupied by a community can vary considerably. Bounded by the distribution of the component species' populations where these overlap, communities produce a uniform species composition. Some species might as well be members of other surrounding (or distant) communities. Like the ecosystem concept discussed in Chapter 5, the *community* concept is broadly defined as one of nested units: conceptually small units potentially being part of containing larger units. This fact is recognized when ecologists define **major communities** as those of sufficient size and completeness of organization to be relatively independent of adjoining communities, and **minor communities** as those more or less dependent on neighboring (or surrounding) assemblages.

Communities show both functional and structural (taxonomic) unity, although some species may be replaceable over time and space so that functionally similar communities can have different species compositions. The community concept emphasizes the idea that organisms live together in an orderly manner; that species distributions are more than simply individuals responding in a similar way to a particular set of physical factors. And, of course, a community has properties or characteristics that are more than the sum of its species populations and unique attributes.

- Read Biocoenosis

Communities and Biomes



A single tree could be considered a community

In simplest terms, a community is an assemblage of populations living in the same place at the same time, interacting with each other and their environment. According to this definition, there are also various spatial scales that are recognized when describing different types of communities. Spatial scale refers to the size of the organisms that make up the community and can range from very small (i.e., bacteria) to very large (i.e., animals). There are three approaches to spatial ecology: **Theoretical Ecology**, **Metapopulation Ecology**, and **Landscape Ecology** (Hanski 1998). Every community affects another adjacent community, i.e. communities intergrade continuously. Read Metapopulation.

Examples of different spatial scales in communities:

- A forest - made up of trees, plants, and animals

- A single tree - made up of a community of insects and flora
- A termite gut - made up of a community of protozoa, bacteria, and archaea

  - Read Communitiy (Ecology).

Emergent properties of communities include stability, response and resilience to invasion and drought, and bioremediation. (Read Bioremediation)

Terrestrial Biomes

The earth contains many different geographical areas that contain similar climatic conditions. As a result of natural selection, many comparable ecosystems, "biomes", have developed in these areas. A **biome** is a community on a global scale, and is usually defined by temperature, precipitation, and by the types of plants and animals that inhabit it. Generally, biome classification is determined by the climate and geography of an area. Each biome consists of communities that have adapted to the different climate and environment inside the biome. Specifically, there are special vegetation adaptations as well as physical and behavioral adaptions made by animals in order to accommodate the environment.



A desert biome near Las Vegas, Nevada

Several biomes have been identified and include **tropical forest**, **temperate forest**, **taiga**, **grassland**, **chaparral**, **desert**, **tundra**, and **aquatic** environments. **Tropical forests** are characterized by high precipitation (around 75–200 cm of rainfall a year) and high temperatures. In contrast, the coniferous forests of the **taigas** get just 30–84 cm of precipitation per year and are exposed to average temperatures of -60 Celsius degrees in the winter. **Chaparrals** also play host to extreme temperatures and low precipitation (15–40 cm of per year) while **grasslands** average 25–70 cm of rain per year and have temperatures similar to those of temperate forest and deserts. **Deserts** and **tundras** are both very dry biomes (less than 30 cm of precipitation per year), but differ widely in their average temperature ranges. While there are clearly a wide variety of biomes on Earth, they are not all equally represented in terms of land mass.



A photo from the Siberian taiga north of Khabarovsk.

Taigas are the largest terrestrial biome covering the Earth's surface. Located in the Northern Hemisphere, just below the tundras, they cover 11% of the land mass in the Northern Hemisphere and make up 27% of the Earth's total forest. In fact, the biggest forest in the world is the Siberian taiga.

Conifers that make up **taigas** exhibit needles rather than leaves as a specialized adaptation for the taiga biome. The needles have less surface area for better water retention and a wax covering with sunken stomata to help reduce water loss and to protect the

conifers from freezing weather. The dark green color of the conifer needles helps absorb energy from the sun to induce photosynthesis for survival. Conifers also display an inverted funnel shape to help shed the enormous amounts of snow load. The long cold winters and the short summers make it hard for plants and animals to survive and the **taiga** biome is consequently less diverse than others. The acidic soil of the **taiga** regions also affects the vegetation and the animals that feed on those plants.



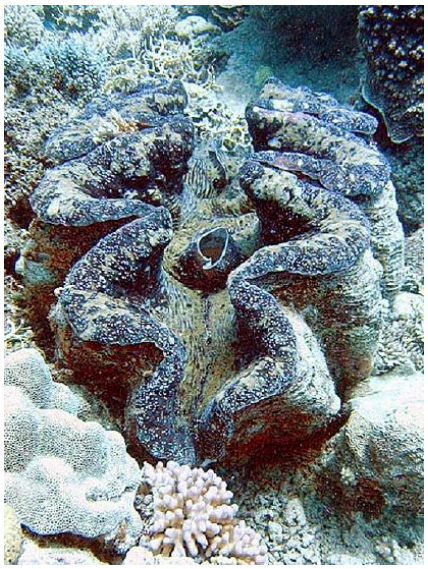
Taiga land surface coverage

The survival and land mass coverage of the **taigas** is threatened by many factors. Since the woody bark of conifer trees is easily burned, fires, natural or man-made, pose a major threat to the **taigas**. Also, logging and clear cutting for pasture land diminishes the size of the **taigas** in certain areas. The province of Manitoba has signed away 40% of its productive taiga for cutting; an area equal to the size of North Dakota. In addition, Alberta, Canada is allowing massive deforestation in the next sixty years. The loss of a considerable portion of the **taiga** is major concern, not only because of the subsequent loss of biodiversity and oxygen production, but also because of the **"greenhouse effect"**. The grasslands are also affected by disturbances. Belcher et al. 1989[1] studied 25 km2 of mixed-grass prairie in Manitoba Canada. The study showed that native prairie was affected by disturbances such as roads, trails, and plowed fireguards. These disturbances expose mineral soil allowing for infestations of leafy spurge which significantly declines the abundance of the dominant native grass species. Leafy spurge poses a threat to potention rangeland, and the conservation of native vegetation.

Aquatic Communities

There are three types of aquatic communities that occur in nature: **marine**, **freshwater**, and **estuaries**.

Marine communities are supported by water of relatively high salinity and are composed of organisms that are able to survive such high-salt conditions. The **tropical coral reef** is an example of a marine community that is usually found in shallow, tropical marine waters in latitudes ranging from 30°N to 30°S. On average, the growth of these communities is limited to depths of less than 100 feet and water temperatures greater than 72 °F (22 °C). These growth limiting factors facilitate the formation of limestone, the major structural component of the reefs. The limestone is secreted by living organisms, including Cnidarians, coralline algae, mollusks, echinoderms, and some annelid worms. Cnidarians are the chief contributor to the limestone formation as they secrete an exoskeleton of calcium carbonate.[2]



A giant clam that is part of the Great Barrier Reef

There are three basic types of coral reefs: **Fringing Reef**, **Barrier Reef**, and **Atoll**. **Fringing Reef** is continuous with the shore line and is usually exposed during low tide. **Barrier Reef** is further away from shore and is usually separated from the shore by a lagoon with an island. The **Great Barrier Reef**, located off the cost of Australia, is the largest known coral reef. Its width varies between 10 and 90 miles along its 120-mile length. **Atoll** is a type of reef that allows some passage out to sea and surrounds a lagoon that does not have an island.

The reefs accommodate organisms of both mobile and non-mobile species. Lobsters, crabs, squid, reef sharks, and many different types of fish and sea cucumbers feed off of the reefs. Different types of algae also inhabit the reefs and serve as a food source for predators.

While the coral reef is an important marine community, many factors are negatively affecting its survival. In fact, as Jackson (1997) points out, coral reef communities have most likely been degraded long before the study of ecology was made relevant in the 1920s. ^ Today, the hulls and anchors of ships associated with the fishing industry are causing damage to the reefs and high demand from the jewelry industry is decreasing the size of the reefs considerably. Coastal development, water pollution and tourism also pose a threat to the success of the coral reef communities. Jackson proposes the need for large scale reef protection efforts with "extreme" political, economic, and social implications if there is to be any hope of reef conservation.^

[3] [http://www.reefbase.org/key_topics/reeffisheries.as}



Barker Dam Lake in California is an example of a freshwater community

In contrast to marine communities, freshwater communities are supported by water of relatively low salt concentration and are composed of organisms that would most likely not survive in high salinity conditions. Freshwater communities include rivers, lakes, streams, and ponds.

An estuary represents a community that is supported by freshwater and saltwater. Estuaries occupy a coastal location, with an open connection to the sea and some type of freshwater flow (i.e., rivers and streams). Therefore, they are affected by the constraints of

both types of environments, creating many small biological niches and accommodating high diversity.



An estuary of the Moore River in western Australia

Due to the variable nature of the salinity in estuaries, there are many factors that must be taken into account during estuary classification. Circulation patterns, tidal range, freshwater input, dominant habitat types, etc., are all examples of potentials for estuary variation. Therefore, estuaries are typically classified by regions (i.e. northeastern United States, southeastern United States). However, as Roman *et al.* point out, each estuary is capable of exhibiting unique characteristics due to the complex nature of the geomorphology of a specific area. ^ Even though regional classifications are generally acceptable, it is important to remember that there are always exceptions to the rule.

Aquatic Ecosystems

Aquatic ecosystems are comprised of two main types: freshwater ecosystems and marine ecosystems. The main driving force of life in these ecosystems is plant growth, from which food chains begin. Plants require four components to grow. They are water, energy in the form of solar radiation (sunlight), inorganic carbon (either carbon dioxide or bicarbonate ions), and minerals/nutrients. Something that we may take for granted is that many of these ecosystems are downstream from humans. However, this fact has not gone unnoticed in the ecosystems. Frissell points out that a number of well monitored species have been detrimentally effected from being downstream of humans. Frissell argues this is due to the fact that we need to view changes to aquatic ecosystems differently than terrestrial ecosystems. Events such as fire and windstorms dramatically effect terrestrial ecosystems, while they have little effect on aquatic systems. At the same time things such as flooding and accelerated erosion are limited in terrestrial ecosystems, but very important in aquatic systems. This is the context in which aquatic ecosystems should be viewed. [4]

Freshwater Ecosystems

The study of freshwater ecosystems is termed limnology. They can be divided into two broad categories: lentic ecosystems, which are contained in basins, and lotic ecosystems, which are flowing water systems. Glaciers are one cause of lentic environments, where retreating glaciers leave behind basins. The flowing water of lotic systems is responsible for about 6 to 30 times the productivity in primary producers compared to primary producers in standing water (Nelson and Scott 1962).

Saltwater Ecosystems

Saltwater ecosystem structures are dictated by temperature, salinity, currents, waves, and tides. The most productive areas of the sea are coral reefs and coastal waters. Freshwater rivers eventually empty into the ocean and terrestrial ecosystems meet the edge of the sea. In certain areas, specifically Australia, there have been increases in salinity in freshwater regions. This has been shown to be a major factor driving natural selection in this region; only the most tolerant organisms are able to survive and reproduce. Unfortunately, it appears that the salinity of these regions will continue to increase. However, the effects of the salinity changes on the ecosystem are unknown and remain to be seen in those areas.[5]

Limnology

Limnology (from Greek: Λίμνη limne, "lake"; and λόγος, logos, "knowledge") is the study of inland waters (both fresh and saline) and their biological, physical, chemical, geological, and hydrological aspects. This includes the study of natural and man-made lakes, ponds, rivers, streams, wetlands, and groundwaters. When studying the dynamics of an ecosystem, limnology involves

variables such as pH, temperature, depth, and dissolved oxygen profiles of the body of water. Productivity of the system is tested using a transparency test with a Secchi disk, or by analyzing species diversity and abundance.

François-Alphonse Forel (1841–1912) established the field with his studies of Lake Geneva, the largest freshwater lake in Europe. Limnology is closely related to Hydrobiology,the science of underwater life, which applies the principles and methods of physics, chemistry, geology, and geography to ecological problems. Much of modern hydrobiology can be viewed as a sub-discipline of ecology, but the sphere of hydrobiology includes taxonomy, economic biology, industrial biology, morphology, physiology, etc. The study of life in inland waters can be divided into **lotic** system ecology (flowing waters) and **lentic** system ecology (still waters).

One area of current research is **eutrophication**, which focuses on biotic interactions in plankton assemblage. This branch of hydrobiology involves microbial loops, water blooms, phosphorus load, and lake turnover. Another concern of limnology is the acidification of mountain lakes. Long-term studies are being carried out to monitor changes in the ionic composition of river, lake, and reservoir water as a result of acid rain and fertilization. Another goal of current research is the elucidation of the basic environmental functions of the ecosystem in reservoirs, which are important for water quality management and water supply.



Fish hatcheries breed fish in a safe environment before releasing them into a lake or river to supplement endangered species or support recreational fishing

Many populations of fish are declining in certain habitats due to environmental changes and recreational fishing. In response, fish hatcheries breed fish in a predator-free, unlimited resource environment before releasing them into a natural habitat, also known as stocking. A study by Power (1994)^ investigated predation by sauger and walleye on paddlefish that were being stocked in Lake Sakakawea. Predators at three different sites along the lake were sacrificed, and 73% had ingested at least one paddlefish. All of the ingested paddlefish still intact were only 36-52% of adult size. These findings suggest that paddlefish are being stocked in the lake before they are large enough to avoid such predation. Another issue with stocking is that the progeny are sometimes genetically inferior to those that are born in a natural habitat. The downfall to raising fish in such an environment is that there is no competition and no "survival of the fittest."

Microorganisms have a huge influence on limnology. They are largely responsible for nitrogen balance in lakes, decomposition of water humus in bogs, annual cycling of iron, and oxidation of sulfur. Kuznetsov (1968)^ studied this complex cycling by incubating reservoirs and using radioactive isotopes of carbon, nitrogen, iron, and sulfur to monitor what form they were in and at what rate turnover occurred. Microorganisms establish an elaborate cycle to maintain chemical stability that allows a variety of aquatic life to flourish.

Succession

The concept of **succession** was first clearly put forth by Clements (1916). The classical use of the term involves three fundamental concepts (after Mitsch and Gosselink, 1986):

1. vegetation occurs in recognizable **communities**;
2. community change through time results from the biota present modifying the environment (changes are **autogenic**);
3. changes are linear and directed towards a **climax** ecosystem (Odum, 1971).

Succession is the predictable and orderly changes in the composition or structure of an ecological community. It's a colonization of a disturbed area that eventually leads to an increase in species diversity. Succession is divided into two stages- (1) Primary Succession and (2) Secondary Succession.



Trees are growing on meadows and fields that are not cultivated anymore

Primary succession deals with the recolonization of bare ground. The primary succession has **r-selected organisms**-- species that can survive at high disturbance areas and are fast growing organisms. There are several factors that can cause disturbance- (1) people, (2) diseases, (3) fire, (4) precipitation/floods, (5) wind/hurricanes/tornadoes, (6) temperature extremes (like freezing or extreme heat), and (7) volcanoes. In other words, the communities that are in early succession will be dominated by fast-growing, well-dispersed species. The other stage of succession (as succession moves forward) will be replaced by more competitive species Wikipedia:en:Ecological succession/Succession. A good example of primary succession is the ecological response to the Mount St. Helens eruption in 1980. Bishop et al. 2005[6] describes that a primary succession landscape like Mount St. Helens may teach us fundamental mechanisms that describe the formation and function of ecological communities. The use and understanding of these mechanisms may lead to the restoration of devastated landscapes.

- Read Wikipedia:en:Seral community

The other stage of succession is **secondary succession** which is the recolonization of partially cleared areas (this occurs after primary succession). Eventually, secondary succession/colonization leads to mature communities called climax communities which are stable communities. The secondary succession communities have **k-selected organisms**--organisms that use the limiting resource the best and therefore can out-compete other individuals. The secondary succession may include a **seral community**--an intermediate stage found in ecological succession in an ecosystem that advances towards its climax community.

- Read Succession

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SECTION OVERVIEW

5.3: Community Succession and Stability

A community can be defined simply as the assemblage of the various special populations occupying the same place at the same time. (See chapter 4 for more details). Therefore, as defined by the Encyclopedia of Earth, community ecology is the branch of ecology that is how interactions between and among species and the abiotic environment affect community structure, including species richness, species diversity, and patterns of species abundance. (See chapter 7 for more details pertaining to species richness and species diversity). One of the most prominent community ecologists is the late Charles Elton. Recently, community ecologists have recognized that the world's flora and fauna are disappearing at alarming rates; such a discovery has led to an increase in investigations researching community stability [1].

Community Stability

Community stability can be defined as the ability of a community to defy change or rebound from change. The concept of rebounding from change is known as resilience. General resilience is a measure of stability that assumes system stability increases as return time to equilibrium/non-equilibrium solution decreases after perturbation/ disturbance. A rapid response means that a system recoils quickly back to its state of equilibrium. The concept of defying changing change is known as resistance. Resistance is a measure of the degree to which a variable changes after a perturbation/ disturbance [2] However, measuring stability in a system can be a difficult task. In 1955, Charles Elton proposed a theory that stated a positive stability-diversity relationship was a result of the stability of aggregate community measures like the total biomass[3]. There is much controversy on the definition of stability and how it is measured.

Stability Diversity Hypothesis

The stability-diversity hypothesis states that the more diverse a community is, the more stable and productive the community is. This hypothesis was formed from the basis that more stable and productive communities can use their resources better and more efficiently as compared to communities of less diversity. There are correlations with stability measures like constancy of community production and community resilience to species loss and also alterations to the relative abundance of different species. Early research has overlooked the possibility that unexpected fluctuations in the abundance of species may be more important than species interactions when it comes to creating stability-diversity associations[4].



Rainforests are diverse communities that may be classified as a type of tropical forest

There are a couple of arguments for and against this hypothesis. An argument for the hypothesis would be that pest outbreaks occur more often on cultivated (disturbed) land. The argument against this statement is that there is no co-evolutionary history with the pests that reside there.

Another statement that can be used to support the hypothesis is that tropical rain forests (which are more diverse) have fewer pest outbreaks than the temperate forests. The argument against this statement is that there is less known about tropical forest as compared to temperate forest, which are heavily studied.

Several experimental tests of the stability-diversity hypothesis have been done. An experiment by Nelson Hairston using bacteria and Paramecium in a two tiered trophic system showed that the extinction rate would decrease with an increase of bacteria species, this result had an increased stability and supported the hypothesis. He also found that the extinction rate increased when there was more Paramecium species present, this result showed an decrease in stability and rejected the hypothesis.

Another experiment to research the stability-diversity hypothesis was done by Tilman. He did a field experiment carried out over eleven years and found that variation in community biomass decreases with increased species richness. But when it came to year to year variation the biomass of a particular species increased with increasing species richness. These results concluded that diversity increases community stability but not population stability. The shortcoming of Tilman's experiment was that he only observed one trophic tier.

- Read Wikipedia:en:Ecological effects of biodiversity

Disturbance

Disturbance can be defined as a change in environmental conditions that affects the stability of an ecosystem. It is any distinct event which ultimately results in the loss of biomass (Huston 1994) and mortality of organisms. According to Sousa disturbances cause patchiness in natural systems. Disturbance renew limiting resources and allow species to coexist. These patches allow for migration between them increasing diversity which ultimately prevents local species from extinction. In areas of local species the absence of disturbance results in a decline in species diversity. These recurrent patchy disturbances are characteristics of most natural systems. Examples include fires in terrestrial plant communities, hurricanes and wind throws in forests, storms over coral reefs, burrowing activity of badgers in prairie grasslands, drift logs which batter the marine intertidal, damage caused by grazing elephants in East Africia, and many more.[5] As can be seen via the disturbance link, wildfires and anthropogenic effects, such as deforestation, are examples of ecological disturbances. Disturbances, such as fire, often initiate succession. It should be noted that succession can be managed. For example, the most important disturbance of Mediterranean forests might possibly be forest fires. Mediterranean forests are a key factor in bio-geochemical cycles, in protection of soil from erosion, regulating water runoff in watersheds, and stabilizing slopes. Therefore, in the recent decade, research and political efforts have been geared towards fire-fighting and returning scorched areas to their pre-fire conditions [6].



Fire is an example of a disturbance.

The connection between community stability and disturbance is one that has been questioned many times. The intermediate disturbance hypothesis suggests that in a community, the highest diversity is seen in communities with intermediate disturbance. And since an increase in diversity equals an increase stability, this hypothesis shows that communities with an intermediate amount of disturbance tend to be the most stable.

The **Intermediate Disturbance Hypothesis** takes into part both benthic and pelagic abilities. The benthic success includes adult survival and reproduction, and the pelagic success involves larval settlement. The amount of coexistence that a dominant species

can tolerate determines how many species can be supported. This hypothesis also states that further settlement by other species is maintained at equilibrium by the balance between settlement, productivity, and mortality but is independent of adult body size. Disturbance increases free space, but settlement decreases it. The three factors that determine the fate of an organism in a habitat are equilibrium free space, disturbance, and settlement. Sufficient settlement with little disturbances yields a habitat that has a stable population.[7]

Problems Determining Stability

In order to determine a community's stability, one must be able to determine the equilibrium point for that community. This may require years of observation. In some cases/communities, the equilibrium point can not be determined because the community is never at an unchanging equilibrium; an example of such a situation is the predator and prey systems. Another problem in determining community stability is in areas that have undergone disturbance but return to equilibrium too quickly. This happens in areas affected by abiotic factors that are under so much stress that they never reach their carrying capacity. If there are alternative stable states, it is sometimes difficult to determine the stability of a population. As a result the community will move towards another equilibrium never returning to its original state.

[[8]]

Charles Elton

Charles Elton was one of the most influential ecologists in history. Born in England in 1900, he studied at Liverpool College and New College, Oxford. He spent most of his time at Oxford. One of his most notable works was the book *Animal Ecology* (1927). This was the first book to give the basic principles of modern animal ecology. Throughout his career he conducted studies on many different species. He published many books and articles many of which were in the *Journal of Animal Ecology* which he founded and edited for nearly 20 years. He also received numerous awards for all his work and was a member of many different scientific clubs. He is recognized as having done more than anyone else to explain the complex interrelationships of different animal communities and their effect on their habitat. Elton died in 1991 in Oxford, England.

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SECTION OVERVIEW

5.4: Invasive Species Ecology

Everyone may not accept what a particular ecologist or group of ecologists deem as "the way things work". Ecology is a relatively young and complex science. As a result, some ecological concepts are based largely on conceptualizing rather than experimentation. It is not easy to test many ecological hypotheses, because it is nearly impossible to control all variables in nature and to replicate nature in controlled settings. The subject or science of "invasive species" involves the basics of ecological thought and has considerable import to global species diversity. However, this is a subject entangled with controversy.



Kudzu, a Japanese vine species invasive in the southeast United States, growing in Atlanta, Georgia

According to Shea Katriona et al. (2002)[1], the Earth's ecosystems are being majorly impacted by biological invasions. She suggests that the invasions can be studied by multiple viewpoints including,**(1)** the characteristics of the invaders,**(2)** the characteristics of the invaded communities,**(3)** resources available, and **(4)** natural enemies. Katriona used the community ecology theory by linking these viewpoints and by applying recent niche concepts with the communities in which they invade, which provides a predictive framework for invasion ecology. The framework presented here, however, shows how core issues of invasion ecology can be introduced into communities and lead to better understanding of the effects of invasion on earth's ecosystems.

Species status and terminology



The mosquito fish can have both detrimental and beneficial effects.

Even for biologists, establishing the ***distributional status*** of a species in a particular location is not always straight-forward. Questions often arise as to what exactly makes a species native as opposed to non-native, because some non-native species have no known negative impacts (Woods and Moriarty, 2001)^ . In fact, sometimes the same species can have both beneficial and detrimental effects. For example, the mosquito fish (*Gambusia affinis*)has been widely introduced around the world because of its suppression of larval mosquitoes, but also has negative impacts on native species of insects, fishes, and amphibians (Colautti and MacIsaac, 2004)^ . Also, natural biological invasions, generally considered range expansions, and introductions involving human activities are important and could be considered a normal ecological process (Vermeij, 2005)^ .

Non-native and native species may be sometimes considered invasive, with invasions often following human-induced landscape changes. The subsequent "damage" to existing ecosystems is simply a value judgment(Foster and Sandberg 2004)^ . For example, various status classifications exist based solely on the location or the discipline that a biologist is working in (Helmreich, 2005). As a result, many important terms relevant to invasion biology, such as "invasive", "weed", or "transient", include qualities that are "open to subjective interpretation" (Colautti and MacIsaac, 2004)^ . Accordingly, attempts to redefine commonly used terms in invasion ecology have been difficult because many authors and biologists are partial to a favorite definition (Colautti and MacIsaac

2004)^ . Also, the status and identification of any species as an invader, a weed, or an exotic are "conditioned by cultural and political circumstances" (Robbins 2005)^

The large number and current complexity of terms used in invasion ecology makes interpretation of the literature challenging and often intimidating. "Exotic", "alien", "transplanted", "introduced", "nonindigenous", and "invasive" are all words that have been used to describe plants and animals that have been moved beyond their native ranges by humans (Williams and Meffe 2005)^ . "Foreign", "injurious", "aquatic nuisance", "pest", and "non-native", are also used as descriptive terms, each with a particular implication. Even the use of what seem to be simple, basic terms to articulate ecological concepts "can confuse ideological debates and undermine management efforts" (Colautti and MacIsaac 2004)^ .

- Read Introduced species (You need follow links only as necessary to clarify terms)
- Read Invasive species (You need follow links only as necessary to clarify terms)

Table 9-1 illustrates the relationships among the most common terms describing species status. Setting aside the obvious difficulty that it is not always certain whether a species is truly native or not native to a particular location (requiring evidence of its presence prior to arrival of humans at that location), the greatest area of controversy involves the division of introduced species into **invasive** and **non-invasive** ("all others" in Table 9-1)because "harm" can be a subjective term based on individual judgement. Although there is a tendency to view "harm" or "pest" largely in economic terms, here we need to focus on the concept in an ecological sense.

Table 9-1. Terms related to introduced and invasive species

<table>
<tr><td>NATIVE</td><td colspan="3">NON-NATIVE INTRODUCED (broad definition)</td></tr>
<tr><td rowspan="2">INDIGENOUS
or ENDEMIC</td><td rowspan="2">CULTIVATED
and
LIVESTOCK</td><td colspan="2">Established in the wild
INTRODUCED
(narrow definition)</td></tr>
<tr><td>INVASIVE
(pest)</td><td>All others
not listed*</td></tr>
</table>

*Not listed in any "official" source as a pest species

- Consult the special glossary for this chapter.

Prevalence of Invasive Species



Acacia baileyana or Cootamundra Wattle is an invasive species on the island of Australia

Invasive species are considered a "significant component of global change" as they cause both ecological and genetic changes in the communities that they invade (Sakai et al. 2001)^ . In fact, the number of species that are transferred from one biogeographical area to another each day is thought to be very large. Also, while the geographic trends and prevalence of these invasive species are not easily predicted, islands tend to contain the largest proportion. On average, though, most countries accommodate about 20% of invasive species in their vegetation. On a global scale, it is estimated that invasive species have come to occupy about 3% of the Earth's total ice-free surface over the last 500 years (Mooney and Cleland 2001)^ .

Invasive Theories

The concept and implications of invasive species and invasion are explained by several ideas, including: **(1)The Biotic Resistance Hypothesis** and **(2) The Invasive Meltdown Theory.**

Biotic Resistance Hypothesis

The **Biotic Resistance Hypothesis** states that species-rich communities are more resistant to invasion because these types of communities are able to use the resources/nutrients more effectively/efficiently than communities with low species-richness.



The native cottontail rabbit among non-native plants like the garlic mustard, mugwort, and burdock

Species diversity, a term related to species richness, is also important to the Biotic Resistance Hypothesis. Species diversity has two components- (1) **Species richness** represented by *s*- which is the number of species in a **community** which is an assemblage of populations, and (2) **Species eveness** represented by *e*- which is the number of individuals of each species in a community.

There are several factors as to why invaders succeed: **(1)** they are highly competitive and which may allow them to reproduce more rapidly **(2)** proximity to the community is a crucial factor dealing with invasion and is divided into two parts- (a) abundance of the invader and (b) distance from the community that is being invaded upon, **(3)** dispersal rate of invaders to new habitat (there may be new migration paths that become available), and **(4)** degree of disturbance.

- Read Wikipedia:en:Invasive Species

Invasive Meltdown Theory



Aerial picture of the Soo Locks between Lake Superior and the lower Great Lakes in Sault Ste. Marie, Michigan, USA

The **Invasive Meltdown Theory** states that as species are added to an ecosystem, each one representing a potential disturbance, the native system is perturbed in such a way that the system reaches a threshold, at which point it cannot resist any further and invasions occur exponentially. Every individual invader is a threat, but it is their collective impact that can cause the greatest damage to a habitat. This phenomenon is termed **invasional cartels**, and creates the conditions for a meltdown.

One illustration of the meltdown hypothesis is the invasion of the great lakes by zebra mussels. The lakes, once incredibly murky, became crystal clear after 15 years of filtering action by the mussels that were brought in on cargo ships from the Black Sea. While the result was desirable, the mussels caused the natural defenses of the lake to be out of flux and the lakes a very easy target for invasion of non-native species. When the amount of species invading the lake are greater than the environment can support, a collapse or meltdown of the entire environment results.

Read more at www.greatlakesinstitute.ca/press/meltdownofthelakes_p.htm



A male Ring-Necked Pheasant at Deer Park, WA.

The counterargument to the meltdown theory involves naturalized species. A naturalized species is one that has become established without any major impact to the environment. Mitchell argues that many naturalized species get a "bad name" from the invasive species that cause a great deal of trouble, such as the zebra mussels mentioned above.[2] A good example of a naturalized species is the Ring Necked Phesant. Intended to be a colony of game birds, it was brought to the mid-west where it flourished without disturbing the native biota. It co-exists with native game birds like partridge and grouse.

Invasive species do not necessarily always have negative effects. For example, in North Dakota, one invasive species is being used to battle another. Leafy spurge is a weed that grows rampant throughout North Dakota and inhibits all other plant life where it grows. The solution to this has been to bring in another non-native species, the flea beetle which feeds on leafy spurge alone. Notably, it has no recorded negative impacts on the environment. Therefore, although it is technically an invasive species, it is being used to keep the North Dakota prairie ecosystem intact.[3]



An Aphthona flava flea beetle is shown here feeding on leafy spurge.

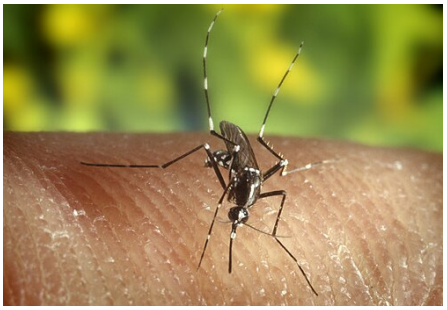
Effects of Invasion

Invasive species have the capability of drastically changing ecosystems, and meanwhile can also affect the human economy. Agriculture, forestry, recreation, and disease are just some examples of issues that can be positively or negatively influenced by invasive species. Sometimes the invasive species|invasive species can be beneficial, and sometimes humans face the nuisance of a troublesome invader.

With the expanding global economy, increasing trade volume and international trade agreements influencing trade worldwide, the risks of "alien" invasions are increasing. The high disturbance of industrial areas increases the disturbances of natural habitats and allow for invasive species to establish. In the last three decades in China, the increasing biological invasions run hand in hand with the increase in economic development (Wen Lin et al. 2007)[4]. In the last three decades China has had a significantly expanded economically with global trade and has consequently been affected by invasive species.

Economic and human factors have both indirect and direct factors which influence the transportation and redistribution of invasive species|invasive species. The increase in global trade by land air and sea has intensified the redistribution of invasive species from places that would normally be isolated. The study of ecological factors on the influence of invasive species are vary rarely studied, and may lead to improving the understanding, predictions, and management of invasive species.

At times, import of an invasive species|invasive speciesis desired for economical benefit, but that species is potentially harmful to another ecological or economical aspect. Much effort is being put into accurately designing risk assessment technologies to determine the net economic benefit of incorporating a nonnative species to an environment. [Keller] Keller *et al.* (2007) analyzed an Australian plant quarantine program (in which plants were used to make ornaments) to develop such a risk assessment program over a wide range of variables. They took into account long-term invasive effects over 10-500 years, and their results indicated that the benefits outweighed the costs in this case. The equation that was developed is: $E_R=((1-a)\theta A+a\theta(1-A))V_T-a\theta(1-A)V_I-D$, where θ is the number of new species,V_T is the benefit of a single species, a is the rate of invasion, V_I is the economic loss caused by an invasive species,A is a proportional accuracy,$D$is the cost of administering the risk assessment preparation and execution, and E_R is the resulting annual net benefit. This equation seems very straightforward and has accurate and even possibly underestimated results for net benefit. However, the terms can be hard to determine, and in the case studied in this project, the annual cost of risk assessment analysis was estimated to be $300,000. This is accounted for, however, by the term D, and is thus incorporated into the equation.



The *Aedes albopictus*, also known as the Asian tiger mosquito,has invaded many countries including the U.S. in the last two decades. It is a common carrier of diseases, including the West Nile virus.

Such risk assessments are important to the balance of economic and ecological success for a case in which incorporation of an invasive species would be necessary.

Invasive pests can kill plants and hamper agriculture, but sometimes can affect the health of animals and even humans. For example, the West Nile virus was never introduced to the Western Hemisphere until 1999, when mosquitoes that carried the disease were somehow transferred across the Atlantic Ocean. Mosquitos are the most prominent insect vectors of disease, and Juliano and Lounibos (2005)[5] used this quality to study the dyanamics of invasive species. The introduction, spread, and impacts of an introduced species can be fairly accurately measured in terms of spread of an associated disease. This particular study focused on the *Aedes albopictus* mosquito. This species was observed under varying conditions, and the effects of competition and predation were measured to determine whether they could slow or prevent invasion. Studies such as this can determine what types of environments (including both biotic and abiotic factors)are susceptible to invasion. This particular project emphasizes that full understanding of such a process must include introduction, spread, and long-term impact of the invasive species. If a study only monitors the current conditions, important dynamics of the system may be overlooked.

Summarization

Although there exists many terms describing what is usually called species **status** for a particular location, most terms are not especially controversial and largely reflect that different disciplines (e.g., agriculture, botany, ornithology, entomology) have developed preferred terminologies for describing essentially the same things.

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SECTION OVERVIEW

5.5: Species Richness and Diversity

Species Diversity Introduction

Species Richness **(s)** is a relative term that refers to the number of species in a community, and is directly associated with measuring the diversity of species in a given area. A related term, evenness (E), is another dimension of diversity that defines the number of individuals from each species in the same area. Together, these terms have been used to describe species diversity patterns on Earth.

There are several hypotheses that have been proposed to explain species diversity patterns. Many of these hypotheses are based upon the idea that species are more diverse near the equator than near the poles. In other words, there is a recognized latitudinal gradient of species diversity on Earth. The hypotheses that support this latitudinal gradient can be divided into two groups: abiotic and biotic. The biotic hypotheses are those that explain species diversity patterns with relation to living organisms. The abiotic hypotheses, on the other hand, explain species diversity patterns with relation to non-living chemical and physical environmental factors.

Abiotic Species Diversity Hypotheses

Four commonly recognized abiotic hypotheses include:(1) **The Time/Stability Hypothesis**, (2) **The Area Hypothesis**, (3) **The Productivity Hypothesis**, and (4) **The Metabolic Hypothesis**.

The **Time/Stability Hypothesis** suggests that diversity is directly related to the length of time that an area of land has been around. Specifically, land that has been around for a long time, undisturbed, tends to have more diversity, and is therefore more stable when compared to land that has been around for a short period of time. For example, the land underneath a glacier that has just receded will be less diverse than land that never had a glacier.

The Area Hypothesis explains species diversity relative to land area. According to this hypothesis, the larger an area is, the more organisms it can support, which results in larger populations. Larger populations are characterized by fewer extinctions and more prevalent mutation events and are, consequently, more diverse.

The Productivity Hypothesis says that the more energy there is in a system, the more biomass there will be in that system. More biomass supports greater species diversity.

The Metabolic Hypothesis states that temperature has an impact on the metabolic rates of organisms. This expands on the idea that every population has a net energy flow that acts upon it. The main idea behind this hypothesis is that larger animals have relatively slower metabolic rates when compared to smaller animals . For example, a mouse must eat half of its body weight to keep from starving, while a human only needs to eat two percent of its body mass to live.

This phenomenon is explained by several ideas. One idea is that larger animals have proportionately less surface area and lose heat more slowly. So, pound for pound, they need less food. The other idea is that larger animals and plants must transport nutrients further and, as a result, use them up more slowly than their smaller counterparts.

The Metabolic Hypothesis, however, suggests that **Temperature** may also have an impact on an animal's metabolic rate. Research shows that a 5˚C rise in body temperature is roughly equal to a 150% increase in metabolic rate. This is true for a large range of organisms, including aerobic microbes, plants, multicellular invertebrates, fish, amphibians, reptiles, birds, and mammals. Gillooly (2001) claims that the metabolic rates of these organisms are all derived from a general function using body size and temperature.



Body size, altitude, and diet account for 99.0% of the variation in the metabolic rates of birds of paradise.

According to **The Metabolic Hypothesis**, organisms with faster metabolic rates have faster mutation rates. This is because they will change quicker and get through more generations more rapidly. Therefore, you would expect to see new species created in small organisms and warm environments.It has also been suggested that body size and temperature predict the density and growth rates of a population. This means that individuals in warmer environments consume resources more quickly, which results in fewer available resources and lower population densities.

The Metabolic Hypothesis has broad implications. According to Brown (2004), the hypothesis is said to be able to predict anything from life history attributes, development rates, mortality rates, and life spans, to rates of competition and predation, population interactions, and patterns of species diversity. In addition, this hypothesis offers an explanation for the peak of biodiversity near the equator.[[1]]

Biotic Species Diversity Hypotheses

There are three commonly recognized biotic species diversity hypotheses. They include: (1) **The Heterogeneity Hypothesis**, (2) **The Competition Hypothesis**, and (3) **The Predation Hypothesis**.

The Heterogeneity Hypothesis suggests that the more spatially diverse the community is, the greater the species richness.

The Competition Hypothesis introduces the concept of **r** and **k** selection. **r-selected organisms** are described as rapid growing organisms that have broad resource requirements and **k-selected organisms** are described as slow growing organisms that have narrow resource requirements.

The Predation Hypothesis says that predation opens up niches and reduces prey. Fewer prey lead to liberated resources which, if used by other species, leads to an increase in species richness. The concept of a **keystone species** is important to this theory. The keystone species is the species that a community is dependent upon and is often a predator. The keystone species maintains stability of the community which will increase species richness.



A hawk is an example of a keystone species as it eats its prey, the mouse

In evolutionary ecology there are many questions regarding variation in species diversity among different areas. In addition to the preeceding abiotic a biotic hypotheses, Emerson (2005)[2] predicts that species diversity can drive speciation and the prediction is supported strongly by the biogeographic theory. By controlling several physical features of the Canary and Hawaiian Islands, Emerson showed that the probability of extinction and speciation for each species on an island increased as the number of species increased. Based on this analysis, species number was positively related to diversification and species richness.

Hutchinson (1959)[3] reports that there are so many animals on the planet because of three reasons: **(1)**The greater the length of food chain (greater species diversity), the more stable the environment is, **(2)** Smaller organisms undergo more evolutionary change due to large populations in which more mutations occur, **(3)** The greater number of niches available, the more species that can occupy them without competition. Communities of greater organism diversity and species richness will persist longer and outlast many communities that are less diverse, and have a shorter food chain.

Rapoport's Rule

Rapoport's Rule, named after Eduardo H. Rapoport, was proposed by George C. Stevens in 1989 as an additional explanation for the already widely accepted notion that species richness has an inverse relationship with latitude. Rapoport's rule introduced the idea that the length of the geographical range of a species, relative to the north and south axis of the earth, plays an important role in the already acknowledged latitudinal gradient of species richness. Specifically, species at higher latitudes have a wider geographical range than species at lower latitudes[4].

The geographical range of a species refers to the range in latitudes, from north to south, in which a species can be found. This range is largely dependent upon climatic stresses in a given region. Accordingly, species in high latitudes have evolved to tolerate extreme and highly variable climatic conditions (i.e. temperature and precipitation) and therefore have a wider geographical range. Species in low-latitudes do not gain a competitive advantage by having such broad climatic tolerances and therefore occupy narrower geographical ranges[5]. This distinction forms the premise behind Rapoport's rule.



Species in higher latitudes evolve to tolerate extreme climatic conditions, resulting in a wider geographical ranges.

Assuming equal dispersal abilities of high and low latitude species, more low latitude species are randomly placed outside of their narrow geographic range than high latitude species. As a result, more low latitude species are placed in environments that they are not well suited for. These species, termed "accidentals", "artificially inflate species numbers and inhibit competitive exclusion.[6]" In other words, "accidentals" would normally be competitively excluded by the better adapted individuals in the same area, but due to the unique nature of narrow tropical geographic ranges, the success of the "accidentals" is only dependent upon their proximity to the areas in which they do well. Therefore, in lower latitudes, more species exist in habitats that they would normally not survive in. In accordance with Rapoport's rule,this phenomenon, called the "rescue effect", accounts for the higher species diversity in the lower latitudes as compared to the higher latitudes[7].

Rapoport's rule, although widely acknowledged, faces criticism from related studies. There is considerable doubt that Rapoport's rule is actually a causatory agent of the latitudinal species richness gradient but is, rather, an artifact of the phenomenon[8][9]. The methods and logic used by Stevens are especially scrutinized, every possible error drawn out[10][11]. For example, it has been suggested that Stevens over-emphasized species richness patterns in higher-latitudes in comparison to lower latitudes, resulting in conclusions that are only applicable to local, rather than regional, patterns. Such gaps in Stevens' methodology and evidence leave Rapoport's rule open to inquiry. Also, many exceptions to the rule have been demonstrated. However, whether or not Stevens' conclusions are completely accurate, Rapoport's rule plays a significant role in the study of species richness patterns and raises questions that promote further studies.

Diversity Measurements

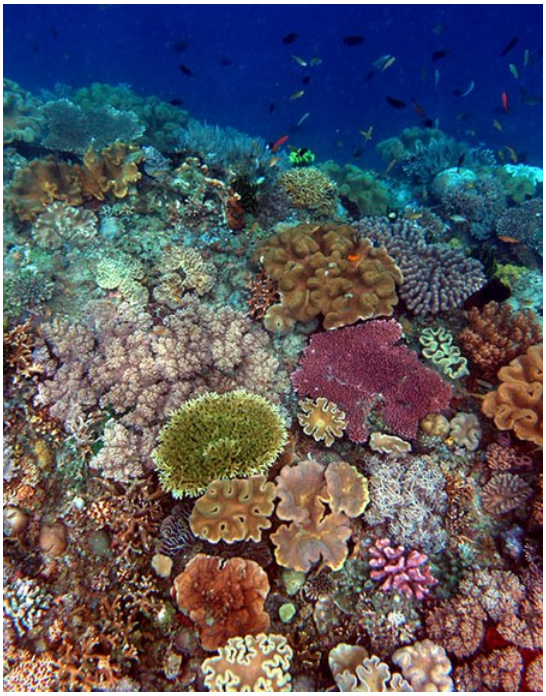
Diversity is measured for three main reasons: **(1)** to measure stability to determine if an environment is degrading, **(2)** to compare two or more environments, and **(3)** to eliminate the need for extensive lists. Diversity indices provide important information about the composition of a community. These indices not only measure species richness, but also take into account the relative abundance

of species, or evenness. When measuring species diversity, species richness and evenness must always both be considered. In addition, indices provide important information about species rarity and commonness in a population. These are important and common tools used by biologists in order to understand community structure.

There are many indicies that can be used to calculate diversity. Some of the more valuable indicies that calculate diversity include the following: (1) **Berger Index**, (2) **Simpson's Index,** [[12]]which calculates the probability that two organisms sampled from a community of will belong to different species, (3) **Shannon-Wiener Index,** [[13]]which accounts for both abundance and evenness of the species present, and (4) **Species Evenness Index**. Each of the indicies uses different mathematical approaches/calculations to test/calculate diversity between two or more communities. These tools for measuring diversity are often used when determining community similarity, ethnic diversity, and biological diversity.

To learn more about the diversity indices, read Diversity index.

In addition to the previous indices, ecologists employ rank abundance curves, which are graphs ranking the most abundant species to the least abundant. They can be shown as a plot of number of species vs. number of individuals on a logarithmic scale that usually yields a normal distribution. This is because environments are usually undersampled, resulting in many singlets,especially in high diversity systems. Singlets make up the middle peak of the distribution, and the more sampling that is performed, the more the curve will shift to the right.



Coral reefs are the home to so many species that undersampling is likely to occur. Estimators can help make up for species that are underrepresented.

The number of unsampled species in cases of undersampling can be roughly estimated using the Chao estimator, in which $S_{estimate} = S_{observed} + F_1^2 / 2F_2$ where F_1 is the number of singletons sampled, and F_2 is the number of doublets. There is also a method of estimating what percent of the total species is represented in a sample, called Good's coverage estimator, in which Coverage = 1 - (number of individuals in species / total number of individuals). These estimator equations allow researchers to have a good idea of how their limited sampling relates to the entire sampled population.

Measurements of species diversity are constantly being improved and/or critiqued by ecologists. Hurlbert (1971)[14] argued that species diversity itself is a "nonconcept" and that theoretic results are not dependable. His view is that ecologists should abandon the "poorly defined" idea of diversity completely, as well as diversity indices, and rely more on direct observation. He came up with alternate equations called "species composition parameters" that are more direct than diversity indices. Although he thought these equations are more reliable than diversity indices, he still stated that they shouldn't be strongly depended upon in research. Soetaert and Heip (1990)[15] also argued that species indices are not always accurate, but worked on finding a way to improve

results. They approached the issue of sample-size dependence of diversity indices. They found that this dependence is highest for more diverse communities and those with more rare species. This is something that can be taken into account during sampling and utilization of the indices. Such endeavors to improve measurements of diversity have and will continue to improve ecological research methods as a whole.

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SECTION OVERVIEW

5.6: Island Biogeography and Habitat Fragmentation

Island Biogeography

Biogeography is the study of the geographic location of a species. Island biogeography is the study of the species composition and species richness on islands.

Island biogeography is a study aimed at establishing and explaining the factors that affect species diversity of a specific community. An island in this context, is not just a segment of land surrounded by water. It is any area of habitat surrounded by areas unsuitable for the species on the island. Other examples of *"islands"* include dung piles, game preserves, mountain tops, and lakes.



Mountain tops are considered islands.

In 1967, ecologists Robert MacArthur and E.O. Wilson, coined the **Theory of Island Biogeography**. This theory attempted to predict the number of species that would exist on a newly created island. It also explained how distance and area combine to regulate the balance between immigration and extinction in an island population. Immigration is the appearance of a new species in a community. Extinction is then the disappearance of a species from a community. This relationship is known as "species turnover", states that the equilibrium value for the island is proportional to the number of immigrants that come to the island, and the loss of individuals due to emigration and extinction.

E.O. Wilson and R. MacArthur did several experiments and made several predictions about the Theory of Island Biogeography. Some of their predictions included (1)species richness tends toward an equilibrium value and (2) the equilibrium value is the result of immigration, but emigration and extinction may also occur.

The equilibrium value (equilibrium diversity value) of an island depends on the area of the island- the larger the area the more resources there are on the island. Smaller islands support smaller populations, and smaller populations are more likely to become extinct. Here is where the **Target Effect** comes in play. The Target Effect says that larger islands have higher immigration rates because they are a bigger target.

Three basic types of species-area relationships have been well defined and demonstrated through various experiments within the field of ecology: "type-1" investigates species richness vs. sample area in nested samples (within a defined habitat or region), "type-2" is defined by examining the total species richness vs. total area among habitats or regions differing in area, and "type-3" examines local species richness in a sample of defined size among habitats or regions differing in area [1].

Another factor that determines the equilibrium diversity value is the distance from the source as discussed below. For example, the immigration rate is higher at closer islands than on islands that are further away from the mainland. Here is where the **Rescue Effect** comes in mind. The rescue effect decreases the rate of extinction due to recolonization and immigration. Immigration is a major contributor due to increasing population size and the size of the genetic pool. These two factors can reduce the probability that any particular species will become extinct [2]. Recolonization happens through two occurrences: Immigration and invasion; immigration is the arrival of a new species to an area, while invasion is the arrival of a species that already inhabits an area [3].

The last factor that contributes and/or determines the equilibrium diversity value is the species richness of the source. Species richness is the number of species in a community. Although islands are considered relatively new land, they can still have a great

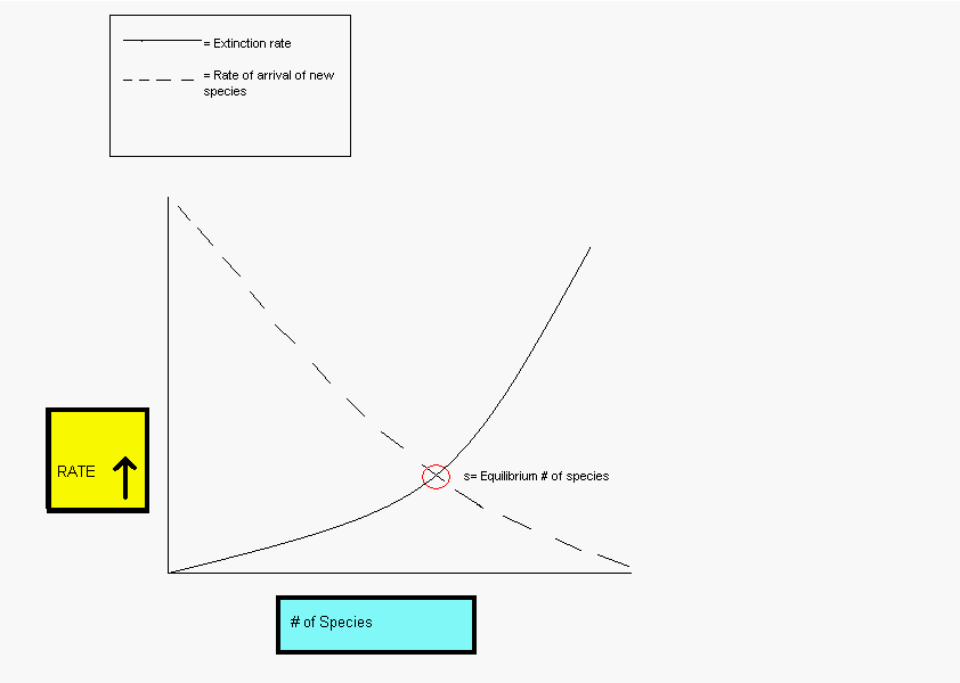
deal of diversity on them over a few years. This concept comes from the **Time/Stability Hypothesis** and to the **Species-Area Effect** which both say that the older the land is/the longer the land has been around, the more diversity and the more stable that land will contain. For example, islands may not be diverse right away because they have not been around long enough for species to migrate onto that particular land mass. The Species-Area Effect states that increased area results in increase species equilibrium. However, this relationship is not linear. The following equation describes this relationship: $S=cA^z$, where S is the number of species, c is a constant, A is the area, and z is the slope of the line (varies).

Islands may be colonized several different ways:(1) by hitchhiking on other species, (2)flying, (3) rafting, (4) swimming, (5) wind, (6) and speciation. It takes time for the new islands to gain several different species of animals due to several different aspects, but given enough time the islands will obtain life on them and become more and more diverse.

Theory of Island Biogeography

The Theory of Island Biogeography is determined by two factors. The first is the effect of distance from the **mainland**. The mainland is where new immigrant species originally inhabited. The second is the effect of island size.

These two factors establish how many species an island can hold at equilibrium. **The equilibrium species number** is the species richness of an island at which immigration balances extinction and which remains roughly constant.



For some examples of island biogeography visit:Island Biogeography

In previous chapters numerous hypotheses have been explored concerning biodiversity. Productivity hypothesis and Rapoport's Rule are major players in the world of ecological biodiversity. These hypotheses have been measured on a continental scale and oceanic scale but how well can they explore the biodiversity of islands? Earlier in this chapter colonization of islands was explained with the effect of size and distance from the mainland. How is diversity affected by the species richness gradient for island geography? Do the same patterns, or lack of, follow islands as they extend from lower latitudes to higher latitudes?

In this section three sets of islands in varying latitudes will be examined. The tropical islands of Kiribati are situated $1^{o}33^{'}$ north of the equator. The Canary Islands in the North Atlantic are located $28^{o}06^{'}$ north of the equator and the Falkland Islands in the South Atlantic at $51^{o}40^{'}$ south of the equator. The biodiversity explored included fauna and flora.

The islands of Kiribati are Gilbert Islands, Phoenix Islands and the Line Islands. Phoenix Islands will be used for this survey. The biodiversity of the islands include numerous fish, birds and wildlife. The Phoenix Islands are the third largest marine biodiversity in the world and in 2006 were protected by the Kiribata government. The island's land biodiversity is not equivalent to the biodiversity of a tropical forest but the diversity in the surrounding water is expansive. Coral Reefs and the distance from any

populous country leave Phoenix Islands undisturbed by tourists. The Phoenix Islands are susceptible to periods of drought which affect the biodiversity of plants and animals. These islands sitting almost directly on the equator support Productivity hypothesis in the water but on land it is not supported due to erratic rainfall. The Canary Islands biodiversity are one of the most expansive in the temperate regions of the world. Scientists studying Canary Islands over the past decades have been discovering a new species or subspecies about every six days. The discovery of new species at this rate makes the Canary Islands an extraordinary example of biodiversity. Twenty-Eight degrees above the equator seems like the ideal place for biomass. The European Union removed internal border checkpoints about ten years ago. Invasive species (chapter 6) have started to take control since the removal of internal borders and have decreased native plant populations by an estimated fifty percent.

The Falkland Islands are the furthest away from the equator at fifty-one degrees south of the equator. The flora on the Falkland Islands are very limited and no trees grow naturally on the islands. The fauna is more diverse than the flora with over sixty types of birds breeding on the islands. Mammals on the island are also limited with three types of seals and smaller mammals and dolphins offshore. The Falkland Islands support the Productivity hypothesis. Moving farther away from the equator diversity is limited. Biodiversity seems to be the greatest not at the equator but approximately thirty degrees north and south of the equator.

Endemism



The Fynbos of South Africa are a great example of Endemism.

Endemism comes from the word endemic which means it is unique to its own place or region and not found naturally anywhere else. The place must be a discrete geographical unit, often an island or island group, but sometimes a country, habitat type, or other defined area or zone. Endemic regions often include large bodies of water, or mountain ranges but mostly islands due to their isolation. Older islands usually have a higher degree of endemism.

Endemic Species can often become endangered or extinct due to their limited habitats and vulnerability to the actions of humans, such as large scale logging and slash and burn techniques. Some ecosystems with high endemism include, the Hawaiian forests, the Fynbos in South Africa, and many other rainforests and dry forests.

Endemic species are also affected greatly by invasive or alien species. Such is the case for the Hawaiian tree snail. The Hawaiian tree snail's existence is being threatened by the loss of habitat via deforestation (an anthropogenic impact) and by the grazing of ungulates, predation by rats, and an intentionally introduced snail, *Euglandina rosea* [4].

Habitat Fragmentation

"[Habitat] fragmentation *per se* is a landscape-level phenomenon in which species that survive in habitat remnants are confronted with a modified environment of reduced area, increased isolation and novel ecological boundaries [5]." **Habitat Fragmentation** is one of the largest causes of species extinctions, along with invasive species. We know that an ecosystem requires land and resources to maintain its diversity, but how much is enough? And when an ecosystem becomes isolated, will the edges of that isolated area remain the same kind of ecosystem as the center?

These questions are studied and answers are inferred through the study of truly isolated habitats: islands.



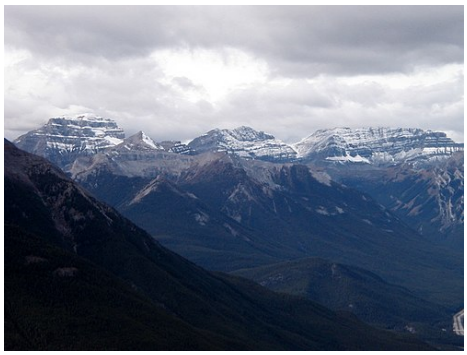
The coyote is a predator that increases with fragmented landscapes.

Islands have less diverse populations than large continents, especially those far from mainlands. Such islands have less opportunity for colonization. In order to apply what we know about islands to fragmented habitats, we must recognize colonization and extinction as constantly occurring within populations.

Anthropogenic or human-derived habitat modification is the largest cause of fragmentation. However, naturally fragmented systems are found all over the world [6]. Habitat fragmentation often results in lack of food and other resources for species that need them. It also eliminates habitat for species that need large unbroken blocks of habitat, examples of species that have this problem as a result of fragmentation are bobcats and upland sandpipers. This results in a increased risk of death by predation because the animal might be forced to venture outside it's patch to find food in order to avoid starvation. Certain predators like raccoons, foxes, coyotes, house cats, and crows tend to increase in fragmented landscapes. This is due to them being highly adaptable and being able to take advantage of the resources available to them. high predation in small patches makes death by predation more common for certain species. This is one of the factors that is contributing to the decline of neotropic songbirds in eastern temperate forest.

Metapopulation Theory

Metapopulation Theory states that several distinct “Patches” are stabilized by their proximity to other patches. A **Patch** is an area inhabited or potentially inhabited by a member of a metapopulation. Patches are usually small areas of land that consist of small populations. The probability of species occurrence in patches is related to the following two factors: habitat destruction and fragmentation[7]. Because the number of individuals in these patches is small, they can very easily become extinct. This results in **demographic stochasticity**, which are fluctuations in population size due to random demographic events.



Mountain tops are an example of a patch in a metapopulation.

The rate at which re-colonization can occur is proportional to the distance between the patches. The further the distance between two patches, the longer it will take for the patch to become colonized again. When one patch has a jump in the number of individuals that inhabit it, the surrounding patches will also be stabilized by the immigration from the species rich patch. The change in a patches inhabitants can be determined by the equation **(dp/dt) =mp (1-p)-μp**; where **P** is fraction of colonized patches,

M is the average recolonization rate, **μ** is the extinction rate, and **1-p** is the uncolonized patches. The metapopulation is stable when the rate at which recolonization is equal the rate of extinction.

Read [Metapopulation]

Links to research: [Eichhornia paniculata] [Maculina arion (the Large Blue Butterfly)]

The classic concept of metapopulation was first mathematically formulated by R. Levin in 1969, but received minute attention until the 1990s when ecologists realized fragmentation of continuous populations into discrete subpopulations was occurring at a high rate.

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CHAPTER OVERVIEW

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6.1: Predation and Herbivory

6.2: Parasitism

6.3: Competition

6.4: Facilitation

6.5: Symbiosis

6.6: Behavioral Biology - Proximate and Ultimate Causes of Behavior

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SECTION OVERVIEW

6.1: Predation and Herbivory

Introduction: Predation

Ultimately, the source of energy for all life originates from the sun. Plants utilize the sun's energy, animals eat plants and utilize the plants' energy, and some animals eat other animals and utilize their energy. The food chain is a cycle of predation, and although it is necessary for life to exist, it has to have limits. Prey develop defenses against their predators, and predators strive to overcome such obstacles. The balance between survival of prey and predator is part of the reason that our ecosystem is so diverse.



The skunk is an example of a prey who uses its chemical defense to scare off predators. The skunk releases a toxin or noxious compound that has a foul smell/odor to it

It is easy to think of predation in the context of common sense. Predator eats prey. However, ecologically, predation is defined as any interaction between two organisms that results in a flow of energy between them [1]. This definition is applicable to both plants and animals. There are four commonly recognized types of predation: (1) **carnivory**, (2) **herbivory**, (3) **parasitism**, and (4) **mutualism**. Each type of predation can by categorized based on whether or not it results in the death of the prey. Carnivory is lethal to the prey, while herbivory and parasitism may or may not be lethal to the prey. Mutualism is not lethal to either predator or prey but, rather, benefits both organisms.



A carnivorous plant has evolved mechanisms of attracting, trapping, and consuming insects

Carnivory

Carnivory is usually the first type of predation that comes to mind when thinking about relationships between predator and prey. Carnivory takes place when a predator consumes meat rather than plants and consequently kills its prey. Organisms that eat meat are accordingly called carnivores. Some types of carnivores do not need to eat meat in order to survive but do so anyway. **Obligatory carnivores**, on the other hand, cannot survive without meat in their diet. **Hypercarnivores** are an extreme example of obligatory carnivores and are able to eat *only* meat due to restricted digestive capabilities. Even though we sometimes associate carnivores with larger animals, carnivorous habits can occur in plants and fungi that feed on insects or microscopic invertebrates. Therefore, the concept of *meat* in the definition of carnivory is open to interpretation.

Carbone *et al.* (2007)[2] used mathematical models to predict prey size limitations for carnivorous mammals. These limitations can be divided into two dietary groups: (1) **small-bodied species**, which feed on prey smaller than themselves, and (2) **large-bodied species**, which feed on prey of approximately the same size. A daily energy expenditure model was developed that incorporates the energy cost of hunting per unit of body mass. The resulting predictions were compared to daily energy intake estimates for 32 species. The results showed consistent differences in energy and time budgets between small and large-bodied species. Specifically, it was shown that energy expenditure by the predator increased with increasing prey size. That is, large-bodied carnivores expend more energy hunting their prey. Carnivores have, therefore, been assigned a maximum possible body mass of one ton. Even though the largest extant carnivore, the polar bear, weighs only about one half of one ton, there are documented extinct species that tipped the scales at nearly one ton. Interestingly, herbivores can grow to be much larger than carnivores, as they don't need to hunt down their prey and often aren't limited in the way that carnivores are. There are extinct herbivores that weighed in at nearly 15 tons!

[[3]] [[4]] [[5]]

Modeling Herbivory

For monophagous herbivores, we use the same model as the Lotka-Volterra Predator-Prey model.

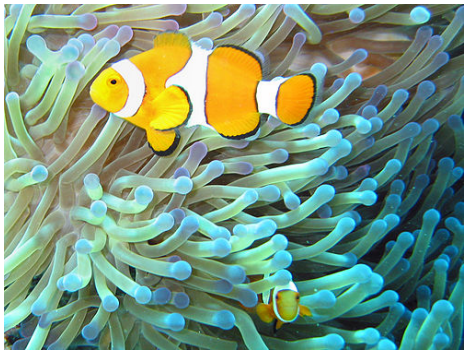
$$\mathrm{dP/dt} = \beta\alpha\mathrm{NP} - \mathrm{mP}$$

For polyphagous herbivores, assuming a constant rate of herbivory,

$dN/dt = rN(1 - N/K) - h$, where h is a constant

In this population, N is dependent upon r and k, where r is the growth rate of N and k is the carrying capacity.

Parasitism and Mutualism



Clownfish and sea anemones have a mutualistic relationship in which the anemone provides a shelter for the clownfish who is immune to its stings, and the clownfish provides the anemone with food.

Parasitism takes place when one organism (**parasite**) benefits at the expense of another (**host**). This type of interaction usually harms the host but, unlike carnivory, does not always result in the death of the host. In most cases, the parasite is much smaller than the host and has a much faster reproductive rate. The tapeworm is an example of a parasite that can thrive in the human digestive system, where it uses nutrients that are important to its host. This often results in weight loss.

Interestingly, it has been proposed that sleep evolved as a defense against parasitism.[6] Studies have been done in which different mammals slept for varying amounts of time. White blood cell counts were subsequently compared, and parasitism rates for different mammals were analyzed. Based on the data, there was a strong correlation between sleep and immune system strength

(white blood cell count). Also, mammals that slept longer were shown to be less prone to parasitic infection. It is questionable whether or not sleep evolved directly to ward off parasitism, but it is clear that sleep has an important role in boosting the human immune system.

Mutualism is similar to parasitism except that the host is not harmed. In fact, both species benefit from the interaction. One example of this type of interaction is called the **endosymbiotic theory**. The endosymbiotic theory suggests that, at some point in the past, an anaerobic cell engulfed an aerobic bacterium, and a mutualistic relationship resulted. That is, the cell provided food and shelter for the bacterium, and the bacterium made additional energy available to the cell. This mutualistic interaction proved so beneficial that natural selection favored these cells. The bacteria that were engulfed are now commonly known as mitochondria. A similar scenario involving a eukaryotic cell (already possessing mitochondria) engulfing a photosynthetic cyanobacterium is hypothesized to have resulted in chloroplasts.

Prey Defenses



Some butterfly species mimic the coloring patterns of their noxious counterparts.

Predation can result in the development of anti-predation strategies by prey populations. Consequently, predator populations develop their own strategies to overcome prey defenses. This phenomenon, known as the red-queen theory, plays an important role in evolution and predator-prey interactions.

Prey defenses can be divided into several different categories. Many organisms utilize **chemical defenses** in the form of toxic or noxious secretions that cause them to taste or smell bad. Most of these organisms exhibit aposematic coloring patterns, which means that they are characterized by distinct markings or bright colorings that signal to the predator that they are toxic and non-palatable (unpleasant tasting). Due to the success of aposematic organisms, organisms that are not noxious, and therefore vulnerable to predation, may exhibit similar coloring patterns to aposematic organisms in order to falsely repel their predators. This is another type of defense called **Batesian mimicry**. Batesian mimicry occurs when a palatable species imitates a non-palatable species. This type of mimicry is only successful if the population of the palatable species is smaller than the population of the non-palatable species. **Müllerian mimicry** occurs when two non-palatable species converge their coloration and patterns for reinforced protection. South American butterflies provide an example of both Batesian and Müllerian mimicry.

For more information, * Read Wikipedia:en:Mimicry

Prey also use coloring patterns to blend into their surroundings. **Crypsis** or camouflage is a means by which organisms use their shape and their coloring to blend into their environment rather than standing out. Clearly, color is an important defense that can be used in multiple ways to protect prey from their predators.

Fighting, **escaping**, and **armor** are three other possible prey responses. Some prey fight back against their predators as a form of self defense. Organisms may also try to **escape or flee** from their predators by using a **startle response** or **indirection**. During this type of defense, the prey perform an action that startles or distracts the predator long enough for them to escape. For example, some toads shoot blood from their eyes, and other animals imitate loud sounds. **Armor** is a form of physical protection. Things such as the shells on turtles, spines or needles on a pufferfish, and thorns on a plant are examples of different types of armor.

Other organisms employ **intimidation** or **threat** techniques that make them appear larger than they really are. Hissing and growling are examples of intimidation techniques that display aggression and create the illusion of an increased threat to predators. **Satiation** and **masting** are intertwined ideas that result in the survival of some prey at the expense of others. **Masting** is more commonly thought of as herding and occurs when organisms travel in very large groups. Because of the size of the groups, predators can only consume so many of them, resulting in the survival of some prey, but not all.

Predation

The predation hypothesis states that predators reduce prey. Fewer prey liberates resources, which in turn are used by other species, which increases species richness. According to Holling (1973),[7] populations of predators and prey often mirror each other. When there is an influx in prey, predator populations tend to rise as well due to an abundance of food. As prey diversity increases, it decreases the likelihood of any single species being overly predated. Therefore this also leads to species richness due to predation. Yoshida et al. supports this idea, and adds that predator density also has a huge impact on species richness. If there is a low predator density, then prey have less of a need to adapt. However, as predator density increases, it forces prey to evolve and to become more resistant to predation, thus forcing more species diversity. Predation also includes the concept of keystone species, or a species that the community is dependent upon, which maintatins stability of the system and increases species richness. Keystone species are often predators, e.g. the African elephant, *Loxodonta africana*, a keystone species of the savannas. One problem this hypothesis encounters is what drives predator diversity.



The African elephant is a keystone species

- Read Predation
- Read Keystone species

The African elephant maintains its habitat by uprooting small trees, which left alone would overtake the savannas and turn them from a grassland into a forest or shrub thicket. By maintaining the grasslands, the elephant ensures the survival of herds of grazing antelope, and the antelope's predators, such as the prides of lions.

The first predator-prey models were proposed in the 1920s by Lotka and Volterra and predict oscillations in populations of predators and prey. Their model was expanded to include heterogeneity so the model could predict actual predator-prey behavior. (Huffaker 1958)

- Read Lotka-Volterra Equation

Mimicry

- read Mimicry

Batesian Mimicry

As a defense against predation some species have evolved to mimic the coloration and patterning of species that are poisonous or less palatable. This type of defense mechanism was first recognized by the English naturalist Henry Bates in 1862.

Müllerian mimicry

Two species that are non-palatable converge on a similar pattern or coloration. This is known as Müllerian mimicry and serves as a reinforcing warning to the predator.

Plant defenses



Cereus alacriportanus uses its mechanical defenses to keep from being preyed on by herbivores.

In their fight for survival, plants have evolved defenses against herbivory. There are three main categories of defense that plants use. The first defensive mechanism is **mechanical defense**, which includes physical features such as thorns and needles. The second type of plant defense is **masting**, which involves producing more progeny than any predators can consume. An example of this is Oak and Beach trees, which release so many cones that they can not all be consumed by predators. The final type of defense is **chemical defense**, which is comprised of five subgroups. The first chemical responses are secondary metabolites. This type defense prevents the herbivore from using its central metabolism to digest the plant. The second type of chemical defense is producing unpalatable taste which keeps predators from consuming the plant. These plants normally contain terpenes and phenolics. Some plants that take advantage of this mechanism are milkweed and mustards. The third type of chemical defense is inhibiting absorption. These plants do not allow the predators digestive enzymes to get absorb nutrients during digestion. The more of the plant that the predator eats the greater the effect will be. An example of plants that use this method are tannins and cumerins. The fourth chemical defense is a plant's ability to make toxins. These toxins are usually alkaloids and cyanides. Deadly nightshade is a plant that uses a toxin to protect itself from any predator. The last type of chemical defense is repellants. These plants usually contain one of the chemicals terpenes or amines. Citronella plants take advantage of this method.

- Read Plant defense against herbivory

Predator-Prey Models

In 1965 Rosenweig and McArthur came up with a predator prey model using linked equations that was a modification of the Lotka-Volterra equation.

$$\frac{dN}{dt} = rN - \alpha NP$$
$$\frac{dP}{dt} = \beta\alpha NP - mP$$

In this model:

N=Prey Species Population

P=Predator Population

α=Predation Coefficient(consists of searching, catching, and consuming)

β=Conversion Factor

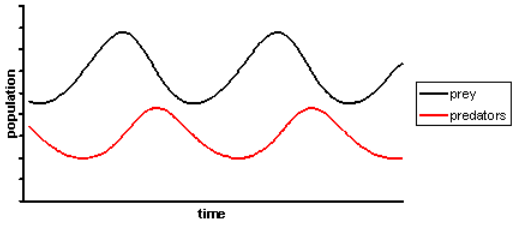
m=Mortality Coefficient

r=Growth Rate

In order to make more sense of these models we need to look at Zero Growth Isoclines(ZGI) also called a Nullcline. This is where $\frac{dN}{dt} = 0$ or $\frac{dP}{dt} = 0$ is set equal to zero. Then the equation it is solved for P or N. To solve for the prey's ZGI you solve for P when $\frac{dN}{dt} = 0$. To solve for the predator's ZGI you solve for N when $\frac{dP}{dt} = 0$.

$$\frac{dN}{dt} = 0$$
$$rN - \alpha NP = 0$$
$$rN = \alpha NP$$
$$r = \alpha P$$
$$P = \frac{r}{\alpha}$$

In order to maintain prey population size at equilibrium, the predator population must increase or become more efficient (α increases) predators. The larger α, the fewer predators that are needed. To maintain P at equilibrium you need N prey; if m is higher you need more N or an increase in $\alpha\beta$. Also, the more efficient P (higher $\alpha\beta$), the fewer N needed. When you plot the prey's ZGI with N as the horizontal axis and P(r/α) as the horizontal axis, you get a horizontal line. When you plot the predator's ZGI on the same graph ($N = m/\beta\alpha$) you get a vertical line. When you plot the vectors for all different populations, you get a stable limit cycle, which also leads to stable oscillations on a graph where N and P are plotted against time. This is also well known as the common Predator-Prey cycle.



There are also a few assumptions that are built into this model:

1. Size of N is limited only by P
2. N is the only food source for P
3. P can consume infinite amounts of N (never satiated)
4. N & P encounter each other randomly
5. P & N age structure is invariant

Predator-Prey cycles are an important part of understanding the relationships between predator and prey. The first realization of this cycle was believed to be noticed by an Italian mathematician named Volterra. Volterra's equations are extensively used in the study of species relationships. Volterra observed Adriattic fishing fleets rise and fall with the numbers of fish caught. As the number of fish (prey) increased so did the number of fisherman (predator) and as the fish decreased so did the number of fisherman. This cycle will eventually repeat itself.

It has also become apparent that Predator-Prey relationships are a major driving force behind evolution. As predator density increases, the number of prey consumed also increases. This forces the prey to adapt to avoid consumption. In other words, the individuals who are better at avoiding consumption live on. Since the better-adapted individuals survive to reproduce, they pass on their survival skills to their young. With a prey population that is becoming better at avoiding consumption, the predators must also adapt to become more efficient. The individuals who cannot capture any prey die off, and the better-adapted population lives on to pass on their traits. This continues in an evolutionary predator-prey cycle.[8]

The Canadian Lynx and Snowshoe Hare are prime examples of a predator-prey relationship. The Canadian Lynx are considered a specialized predator: they will try to only feed on the Snowshoe Hare. Since the 1720s the Canadian government and the Hudson Bay Company have been keeping meticulous records of the rise and fall of Lynx and Hare numbers. Every eight to ten years, the cycle can be observed. Another excellent example of these relationships is the predation of lemmings in the high-Arctic tundra in Greenland. The lemmings have 4 main predators: the arctic fox, the snowy owl, the stoat, and the longtailed skua. This is a highly observed relationship because the number of prey has no limits other than predation. This means that they have an unlimited habitat

available to them and an unlimited food source. Since there are no other factors contributing to the number of prey, scientists are able to find many relationships between predator and prey, such as which predators are more efficient during high and low prey densities, which predators are more effective during certain seasons, and so on.[9]

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SECTION OVERVIEW

6.2: Parasitism



This is an example of a parasite that can cause Chagas disease

Symbiosis is a form of living in which two organisms that are phylogenetically different (unrelated) co-exist over a long period of time (usually for the lifetime of one of the individuals). There are several different outcomes of symbiosis. When a symbiote lives with another organism, this can cause commensalism, which is defined as two organisms that co-exist in the same space, with one of the organisms benefiting from the other while neither harming nor helping the other organism. Symbiosis may also take the form of mutualism, in which both organisms benefit. Parasitism occurs when the symbiote (which is usually a smaller organism) benefits from the other organism (the host), which is harmed, sometimes lethally.

The term parasite has come to mean a eukaryotic, pathogenic organism. Some parasites require the use of **vectors**, such as insects, that carry the parasite to a reservoir.

It is a fact that nearly half of all the animals have at least one parasitic phase in their life cycles. Essentially all free-living animals are host to one or more parasitic taxa at some point in their lives.

Examples of Parasites



Mistletoe is an example of a plant parasite

Some examples of endoparasites include *Giardia lamblia* , an anaerobic protozoan parasite which reproduces via binary fission. It affects humans, cats, and dogs, among other wild animals. Another endoparasite is the hookworm, either *Ancylostoma duodenale* or *Necator americanus*, which infects humans.

Examples of ectoparasites include the Rocky mountain wood tick, Dermacentor andersoni, and a mosquito. Mistletoe, is an example of an epiparasite, called an aerial parasite. A plant parasite is a parasite that attaches to the branches of trees or shrubs.

Types Of Parasitism



Example of a endoparasite

There are several different types of parasites. Parasites that live in the body are called **endoparasites**. An example of an endoparasite is a hookworm that lives in the host's gut. Parasites that live on the outside of the body are called **ectoparasites**. An **epiparasite** is a parasite that feeds off another parasite; this is called **hyperparasitism**. An example of this situation is a wasp or fly larva being an endoparasite in a wasp larva and the wasp larva being an endoparasite in a wood boring beetle larva.

Endoparasites get access to the host's body through an organism's tissue and through ingestion of raw foods. An example of an organism that gains access through raw foods is the nematode *Ascaris lumbricoides*. It gains access to the human intestine, where it produces large numbers of eggs that are passed out of the host's digestive tract to the external environment, where they may be inadvertently ingested by humans in places without good sanitation.

- [Examples of Parasitism]
- [Parasites]
- [Parasitism in Plants and Animals]

Plasmodium, the protist that causes malaria, is a parasite of humans using the *Anopheles* mosquito as its vector.

Most **epiphytic** plants do not harm their host and do not use nutrients from the host, but some, such as mistletoe, are parasitic. The berries from mistletoe are covered with a sticky laxative coating and are spread by birds. These seeds develop haustorium when germination begins and penetrate the bark of young trees. Lethal infections can subsequently occur.

Brood Parasitism



The Goldeneye duck lays its eggs in the nests of other females.

Organisms called Brood parasites[1] use the strategy of brood parasitism, which is often an overlooked type of parasitism. This involves the use of host individuals of the same or different species to raise the young of the brood parasite. This therefore leaves the parasite with no responsibility of rearing their young. This leaves them more time to focus on other things such as producing more offspring. The most common types of brood parasites are usually birds and insects. A couple of examples of birds are the Brown-Headed Cowbird, and the Goldeneye duck. Cuckoo bees and wasps are some examples of insects that are brood parasites.

The Cowbird family is the bird family in North America that is an obligate brood parasite (one that must parasitize because they are not capable of building a nest). While most brood parasites have eggs that mimic the host's, eggs the cowbird is again different. The

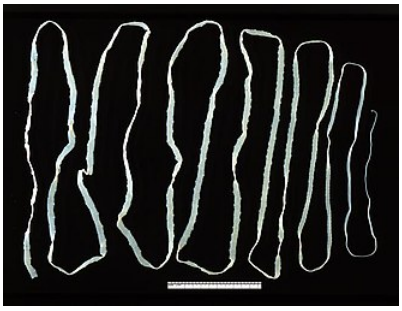
cowbird has been documented to have used over 200 different host species.

Parasitoidism

This phenomenon usually occurs in wasps, where the parasitic association usually results in the death of the host. A wasp will lay her eggs in front of, on, or in another insect, sometimes a grub. The larvae hatch inside of the grub, feeding on it and growing, until they burst out of the organism, killing it in the process.

The Host

The most important aspect of the parasite's life is the selection of a host. Without a host species the parasite does not and can not survive. For a parasite to survive, the host is required to complete the life cycle for the parasite. Since this is a vital part of the parasite's livelihood, the parasite will rarely kill their host species. Unfortunately for both parties, the simple presence of a parasite can cause much harm to the host. The choice of a host species is observed through host specificity and host range.



A full-grown tapeworm that infects humans and lives in the small intestine

Host specificity is seen whenever a parasite is supported by only a single host. The host specificity of a parasite is very important to parasites that flourish only in certain environments and conditions. Many parasites in fact are limited to only one or a few closely related host species. Even though it is possible for a parasite to infect different types of species, they still tend to parasitize certain species more than others. An example of this occurrence can be seen in the parasitic flatworm *Monogenea*. The *Monogenea* have been known to be parasitic on teleosts, elasmobranchs, amphibians, and reptiles. However, the highest concentration of these flatworms has been seen on the teleosts(ray-finned fishes). The *Monogenea* show high host specificity for the teleosts.

The host range of a parasite is when that organism is supported by a number of host species. It is also a measurement of the range of host species a parasite will/can infect. An example of a parasite that has a wide range of host species is the common mosquito that not only parasitizes humans, but other animals as well. The mosquito requires the blood of other animals to sustain its life cycle. Host specificity and host range can be compared to the concepts introduced in Chapter 11, Ecology/Predation and Herbivory, that discusses monophagous and polyphagous herbivores that either eat one species of plant and are dependent on that food source or eat many species of plants to have a wider range of possible sustenance.

Some parasites can manipulate their host's behavior; a good example of a parasite with this manipulation ability is the hairworm. Their lifecycle consists of a transition from an aquatic habitat, where they live off aquatic insect larvae, to a terrestrial habitat where they live off crickets and or grasshoppers. Studies of crickets infested with mature hairworms have shown that the crickets are more likely to seek water. This is when the hairworms have reached their free living stage. Once the crickets reach the water the hairworms emerge and cause the crickets to struggle about the water. This process causes an increase of predation by fish to prey on the struggling crickets [2].

Host Defenses

Hosts have evolved various adaptations to combat parasites initial infection and proliferation. These adaptations can be as complex as antigen specific cell mediated responses, which are most common in vertebrates, or simpler, like barrier mechanisms. Hosts also have behavior defenses that reduce the chances of an individual coming in contact with a parasite. Parasites can have an effect on host life-history evolution, sexual selection and also population dynamics [3].

There are two kinds of host immunities; **adaptive immunity**, whereby the host produces antibodies which are parasite-specific, and **Innate immunity**, which are non-specific. Some techniques a host may utilize to defend against parasites include evasion, preening, grooming, and self medication.

Evasion is one of the first immune defense host response against infection as it imposes several barriers to viral replication and spread [4]. The most common type of evasion is when we have a viral or bacterial infection and your mucus glands work to excrete the infection through the nearest exit, such as the nose. Another interesting example of evasion can be found in *Infection and Immunity* Journal at:[[5]]

Preening is a way to reinforce cospeciation between the host and the parasite. This happens when the host and parasite speciate in tadem, generating congruent phylogenies. To learn more visit:Host defense reinforces host–parasite cospeciation

Grooming is a very common way for hosts to control parasites. An example would be primates sitting together picking them off each other and eating them. Self-medication could be a possibility also: a host could eat a type of plant that might force an evasion.

Certain ectoparasites decrease the reproductive success of breeding birds; an example of one of these ectoparasites is Blow flies Protocalliphora spp., which cause a direct loss of nutrients to the nestlings. Some nestling birds use dietary nutrients such as carotenoids to lessen the effects that parasites have on them [6].

Parasite Community Effects

The effect of a parasite on the host population can cause an epidemic (outbreak) of a disease in a community. Some diseases may show cycles similar to predator-prey cycles. This shows the struggle that occurs between parasites and their hosts. In humans, whooping cough and measles are examples of diseases where parasites infect hosts. Hosts that have never been infected are susceptible to a disease the first time, but after that they are non-susceptible to the infectious host. After an outbreak enough of the hosts in the community become immune to the disease and the disease will decline in the population. This will cause the epidemic to be wiped out and it will not return until there are a number of new individuals born or new immigrants brought into the community.



A mosquito is a parasite that can infect its host with a disease.

Disease Model: Rp=SBL

- Rp: The replacement rate of infected hosts.
- S: The density of the susceptible host.
- B: Transmission rate
- L: The average period during which a host will be infectious.

When Rp has a value that is equal to or greater than 1 the outbreak will return in the community. This will start the cycle over again since once there are more non-susceptible hosts the outbreak will die off again. When the disease affects children the cycle will happen very rapidly do to the high turnover rate. When a disease is fatal to an individual host population, the host can be limited and controlled. This means that something as small as a parasite can control the population of large animals.

Parasites can also have an effect on competition between two species. There are some species that compete for food and resources, and parasites can give some species an advantage. One example is white tail deer and their immunity to Parelaphostrongylus tenuis. While the white tail deer are immune to the disease, moose, mule deer, and pronghorns are not immune. This means that the population of these species can be controlled by the parasite that has infected them. Probably the most well known example of parasitism is malaria which is caused by the mosquito.

Read: [Parasitism]

Phoresis

Phoresis is a defined behavior in which less mobile parasite species hitchhike on other, more mobile parasite species. An example of such behavior can be seen in the interaction between feather-feeding lice and louse flies. However, it should be noted that not all species of feather-feeding lice engage in such behavior. Feather lice (Phthiraptera: Ischnocera) are wingless. They are also permanent parasitisers of birds. Transmission to new hosts is made possible by catching a ride (hitchhiking) on parasitic louse flies. Louse flies do have wings and fly between individual hosts. Because every host eventually dies, phoresis, an evolved mode of transmission, is essential for the persistence of many parasite lineages [7].

Parasitic Castration

The specific blocking of host reproduction by a parasite is known as parasitic castration. This host-parasite interaction is intensity-independent, meaning a single parasite can bring about the blocking of the host's reproductive capability. Parasites benefit from parasitic castrations by diverting the energy a host puts forth in reproduction into their own growth and reproduction. The most studied parasitic castration systems involve invertebrates, particularly crustaceans, echinoderms, and molluscs. Parasitic castrations of vertebrate hosts have been seldomly recognized. In a recent study, it has been demonstrated that a common external cymothoid isopod, *Anilocra apogonae*, castrates Indo-Pacific reef fish host *Cheilodipterus quinquelineatus* [8].

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6.3: Competition

Resources are often limited within a habitat and multiple species may compete to obtain them. **Competition** occurs when organisms use the same resources, and one or both organisms is harmed. Competing species are often occupy the same trophic level and compete for food, but species on different trophic levels could still compete for space, water, etc. **Intraspecific competition** occurs within a species. For example, most penguins defend territories from other individuals of the same species because they compete for suitable habitat and other resources (figure **6.3.*a***). **Interspecific competition** occurs between different species. For example, the **invasive** vine, kudzu, competes with trees in the southeastern United States for light (figure **6.3.*b***). Kudzu is considered invasive in this region because it occurs outside of its historical range (Asia and Australia) and causes ecological harm.



Figure **6.3.*a***: Adélie penguins at Cape Adare in Ross Sea, Antarctica. These penguins defend small territories in which they nest. Image by Brocken Inaglory (CC-BY-SA).



Figure **6.3.*b***: Kudzu is a vine that covers trees, shrubs, and other structures. It can fully block its competitors' access to light, eventually killing them. Image by Katie Ashdown (CC-BY).

Ecologists have come to understand that all species have an **ecological niche**: the unique set of resources used by a species, which includes its interactions with other species. The **competitive exclusion principle** states that two species cannot occupy the exact same niche in a habitat. In other words, different species cannot coexist in a community if they are competing for all the same resources. Competition harms one or both competitors because it wastes energy. In an experimental test of competitive exclusion, two species of the freshwater microbe *Paramecium* were cultured separately and together. When cultured separately, both species

reproduced, and the number of cells (individuals) increased. However, when the two species were grown together, one species (*P. aurelia*) grew, and the the other species (*P. caudatum*) was eliminated. Because both species occupied the same ecological niche, they could not coexist. *Paramecium aurelia* was the superior competitor in this case (figure **6.3.*c***). Competitive exclusion may be avoided if a population evolves to make use of a different resource, a different area of the habitat, or feeds during a different time of day. This is called **resource partitioning**. The two species are then said to occupy different microniches. These species coexist by minimizing direct competition.

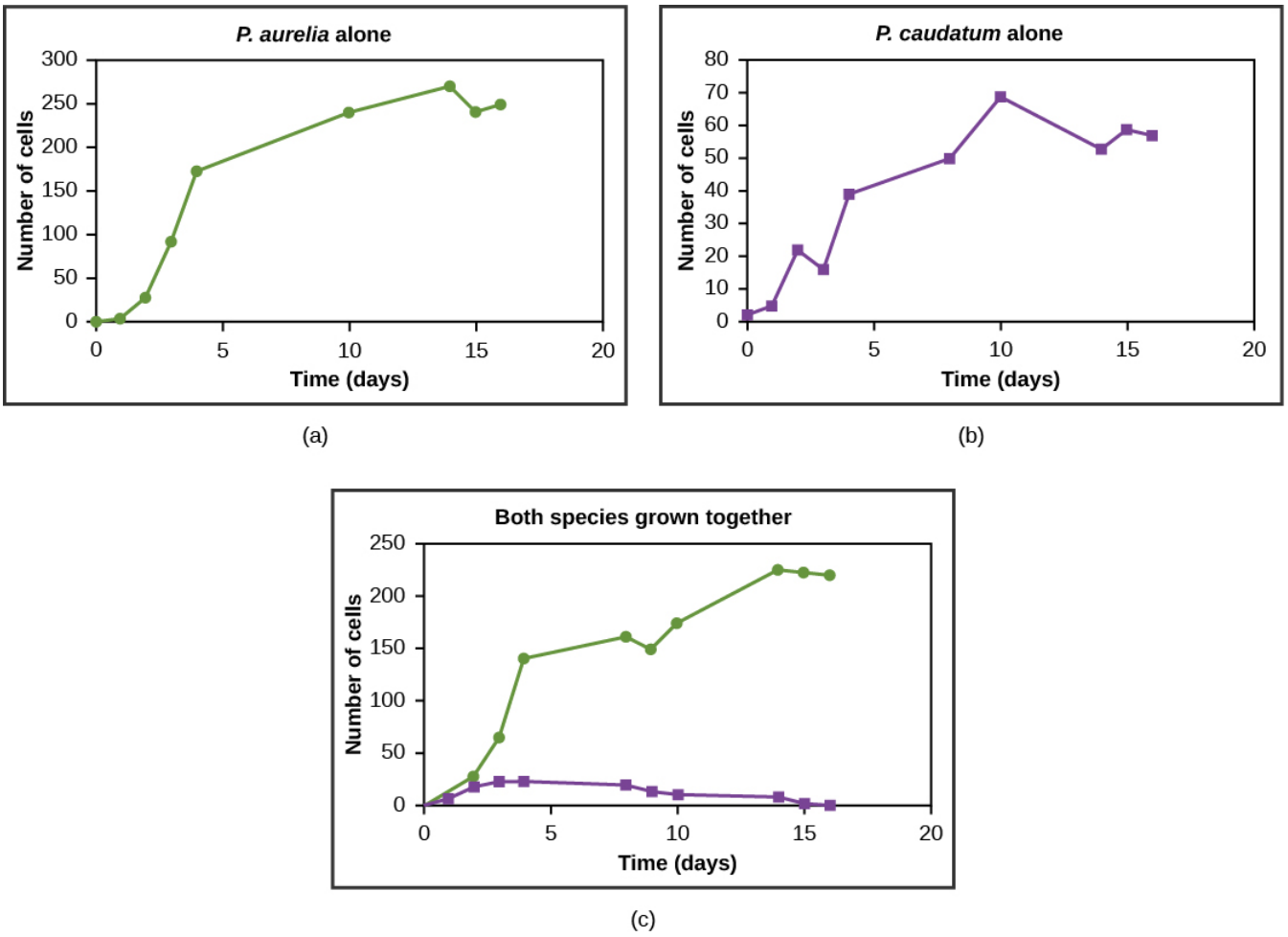


Figure **6.3.*c***: Graphs a, b, and c all plot number of cells versus time in days. When *Paramecium aurelia* and *P. caudatum* were grown individually in the laboratory (a and b), the two species both reproduced and reached a relatively high cell density. When the two species were placed together in the same test tube (habitat, c), *P. aurelia* (top, green) reached nearly the same cell density as it exhibited when grown alone, but *P. caudatum* (bottom, purple) hardly grew at all, and eventually its population drops to zero. *Paramecium aurelia* outcompeted *P. caudatum* for food, leading to the latter's eventual extinction.

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6.4: Facilitation

Interactions in which one or both species benefit and neither is harmed are called facilitation. There are two types of facilitation: commensalism and mutualism.

Commensalism

Commensalism is a type of facilitation that occurs when one species benefits from an interaction, while the other neither benefits or is harmed. Many potential commensal relationships are difficult to identify because it is difficult to demonstrate that one partner is unaffected by the presence of the other. Birds nesting in trees provide an example of a commensal relationship (figure **6.4.*a***). 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.



Figure **6.4.*a***: 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)

Another example or a commensal relationship involves the Little Blue Heron and the White Ibis, which are both wading birds. The Little Blue Heron catches more fish in the presence of the White Ibis, but the White Ibis is unaffected. Interestingly, Little Blue Herons attempt to catch fish more often in the presence of the species, but the success rate of their attempts does not change. Nevertheless, more frequent attempts still increases the total number of fish caught. The White Ibis may make fish more visible to Little Blue Herons, causing changes in their behavior (figure **6.4.*b***).



Figure **6.4.*b***: The Little Blue Heron (left) and the White Ibis (right) have a commensal relationship. Image by Russ (CC-BY).

Mutualism

In a **mutualism**, both species benefit from their interaction. For example, pollinators, such as bees, butterflies, and hummingbirds, benefit because they eat the collect pollen and/or nectar that they collect from flowers. The plants also benefit because their pollen is dispersed to other plants, allowing them to reproduce. Both the pollinators and the plants benefit, demonstrating a mutualism (figure **6.4.*c***). Clownfish and anemones are another example of mutualisms. Clownfish gain protection from living among anemones. In return, clownfish clean the anemones and scare away predators. In addition, their waste provides nutrients (figure **6.4.*d***).



Figure **6.4.*c***: A male Broad-Tailed Hummingbird visits a scarlet gilia flower at the Rocky Mountain Biological Laboratory. The hummingbird gains food (nectar) while aiding the gilia flower with reproduction. Image by David W. Inouye (CC-BY).



Figure **6.4.*d***: These clownfish have a mutual relationship with the sea anemones in which they live. Image by Samuel Chow (CC-BY).

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6.5: Symbiosis

Some biological interactions are brief, such as predation. In others, species are closely associated for long periods. Such associations are called **symbiotic** ("living together"). One species always benefits in a symbiosis, but the other may be harmed (parasitism), unaffected (commensalism), or benefited (mutualism). Some experts considered all parasitisms, commmensalisms, and mutualisms to be symbiotic, but others only consider interactions in which species are living together in a close association (such as when one species lives on or in the other) as symbiotic.

Termites have a symbiotic relationship with microorganisms called protozoa that live in the insect's gut (figure **6.5.*a***-a). The termite benefits from the ability of the protozoa to digest cellulose, a carbohydrate important in plant structure. However, the protozoa 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 symbiotic relationship between a fungus and algae (or a photosynthetic bacteria; Figure **6.5.*a***-b). In lichen, the algal cells are fully surrounded by the fungus. The sugars produced by the algae through photosynthesis provide nourishment for both organisms. The physical structure of the fungus protects the algae from the elements and makes certain nutrients in the atmosphere more available to the algae. The algae of lichens can sometimes live independently given the right environment, but many of the fungal partners are unable to live on their own. Note that while both lichen and the example involving termites mutually benefit the species involved, symbioses are not always mutualisms.



Figure **6.5.*a***: (a) Termites form a symbiotic relationship with protozoa living in their guts. Their association which allows 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)

The remora and the shark is a commensal symbiosis. The top fin of the remora is modified into a sucker with which it forms an attachment to the shark. When the shark feeds, the remora picks up scraps. Additionally, the remora gains transportation and protection. The shark makes no attempt to prey on the remora and is unaffected by it (figure **6.5.*b***).



Figure **6.5.*b***: A remora attached to the top of a shark in an aquarium. This is an example of a symbiosis because the remora lives in close association with the shark. Image by Brian Snelson (CC-BY)

There are many additional examples of symbiosis. Coral are small animals that harbor photosynthetic microorganisms called dinoflagellates. (The corals group together and deposit hardened calcium carbonate skeletons.) **Mycorrhizae** are fungi that surround or live within plant root cells and help plants absorb nutrients from the soil in exchange for sugars. In fact truffles are often found in oak forests because the fungus that produce this spore-forming body establishes mycorrhizae on oak roots. **Root nodules** are structures on the roots of legume plants that house nitrogen-fixing bacteria (see The Nitrogen Cycle). **Epiphytes** are plants adapted to live on top of other plants and are common in the tropical rainforest (see Biomes). Humans have a diversity of microorganisms, called the **normal flora**, that live in and on our bodies. While we often think of bacteria as causing infection (a parasitism), the species of our normal floral exemplify commensalism and mutualism. For example, our gut microbiota aids with digestion and helps us synthesize certain vitamins.

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6.6: BEHAVIORAL BIOLOGY - PROXIMATE AND ULTIMATE CAUSES OF BEHAVIOR

LEARNING OBJECTIVES

By the end of this section, you will be able to do the following:

- Compare innate and learned behavior
- Discuss how movement and migration behaviors are a result of natural selection
- Discuss the different ways members of a population communicate with each other
- Give examples of how species use energy for mating displays and other courtship behaviors
- Differentiate between various mating systems
- Describe different ways that species learn

Behavior is the change in activity of an organism in response to a stimulus. Behavioral biology is the study of the biological and evolutionary bases for such changes. The idea that behaviors evolved as a result of the pressures of natural selection is not new. For decades, several types of scientists have studied animal behavior. Biologists do so in the science of ethology; psychologists in the science of comparative psychology; and other scientists in the science of neurobiology. The first two, ethology and comparative psychology, are the most consequential for the study of behavioral biology.

One goal of behavioral biology is to distinguish between the innate behaviors, which have a strong genetic component and are largely independent of environmental influences, from the learned behaviors, which result from environmental conditioning. Innate behavior, or instinct, is important because there is no risk of an incorrect behavior being learned. They are “hard wired” into the system. On the other hand, learned behaviors, although riskier, are flexible, dynamic, and can be altered according to changes in the environment.

INNATE BEHAVIORS: MOVEMENT AND MIGRATION

Innate or instinctual behaviors rely on response to stimuli. The simplest example of this is a reflex action, an involuntary and rapid response to stimulus. To test the “knee-jerk” reflex, a doctor taps the patellar tendon below the kneecap with a rubber hammer. The stimulation of the nerves leads to the reflex of extending the leg at the knee. This is similar to the reaction of someone who touches a hot stove and instinctually pulls their hand away. Even humans, with our great capacity to learn, still exhibit a variety of innate behaviors.

KINESIS AND TAXIS

Another activity or movement of innate behavior is kinesis, or the undirected movement in response to a stimulus. Orthokinesis is the increased or decreased speed of movement of an organism in response to a stimulus. Woodlice, for example, increase their speed of movement when exposed to high or low temperatures. This movement, although random, increases the probability that the insect spends less time in the unfavorable environment. Another example is klinokinesis, an increase in turning behaviors. It is exhibited by bacteria such as *E. coli* which, in association with orthokinesis, helps the organisms randomly find a more hospitable environment.

A similar, but more directed version of kinesis is taxis: the directed movement towards or away from a stimulus. This movement can be in response to light (phototaxis), chemical signals (chemotaxis), or gravity (geotaxis) and can be directed toward (positive) or away (negative) from the source of the stimulus. An example of a positive chemotaxis is exhibited by the unicellular protozoan *Tetrahymena thermophila*. This organism swims using its cilia, at times moving in a straight line, and at other times making turns. The attracting chemotactic agent alters the frequency of turning as the organism moves directly toward the source, following the increasing concentration gradient.

FIXED ACTION PATTERNS

A fixed action pattern is a series of movements elicited by a stimulus such that even when the stimulus is removed, the pattern goes on to completion. An example of such a behavior occurs in the three-spined stickleback, a small freshwater fish (Figure 45.34). Males of this species develop a red belly during breeding season and show instinctual aggressiveness to other males during this time. In laboratory experiments, researchers exposed such fish to objects that in no way resemble a fish in their shape, but which were painted red on their lower halves. The male sticklebacks responded aggressively to the objects just as if they were real male sticklebacks.

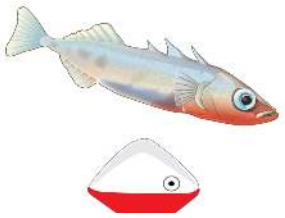


Figure 45.34 Male three-spined stickleback fish exhibit a fixed action pattern. During mating season, the males, which develop a bright red belly, react strongly to red-bottomed objects that in no way resemble fish.

MIGRATION

Migration is the long-range seasonal movement of animals. It is an evolved, adapted response to variation in resource availability, and it is a common phenomenon found in all major groups of animals. Birds fly south for the winter to get to warmer climates with sufficient food, and salmon migrate to their spawning grounds. The popular 2005 documentary *March of the Penguins* followed the 62-mile migration of emperor penguins through Antarctica to bring food back to their breeding site and to their young. Wildebeests (Figure 45.35) migrate over 1800 miles each year in search of new grasslands.



Figure 45.35 Wildebeests migrate in a clockwise fashion over 1800 miles each year in search of rain-ripened grass. (credit: Eric Inafuku)

Although migration is thought of as innate behavior, only some migrating species always migrate (obligate migration). Animals that exhibit facultative migration can choose to migrate or not. Additionally, in some animals, only a portion of the population migrates, whereas the rest does not migrate (incomplete migration). For example, owls that live in the tundra may migrate in years when their food source, small rodents, is relatively scarce, but not migrate during the years when rodents are plentiful.

FORAGING

Foraging is the act of searching for and exploiting food resources. Feeding behaviors that maximize energy gain and minimize energy expenditure are called optimal foraging behaviors, and these are favored by natural section. The painted stork, for example, uses its long beak to search the bottom of a freshwater marshland for crabs and other food (Figure 45.36).



Figure 45.36 The painted stork uses its long beak to forage. (credit: J.M. Garg)

INNATE BEHAVIORS: LIVING IN GROUPS

Not all animals live in groups, but even those that live relatively solitary lives, with the exception of those that can reproduce asexually, must mate. Mating usually involves one animal signaling another so as to communicate the desire to mate. There are several types of energy-intensive behaviors or displays associated with mating, called mating rituals. Other behaviors found in populations that live in groups are described in terms of which animal benefits from the behavior. In selfish behavior, only the animal in question benefits; in altruistic behavior, one animal's actions benefit another animal; cooperative behavior describes when both animals benefit. All of these behaviors involve some sort of communication between population members.

COMMUNICATION WITHIN A SPECIES

Animals communicate with each other using stimuli known as signals. An example of this is seen in the three-spined stickleback, where the visual signal of a red region in the lower half of a fish signals males to become aggressive and signals females to mate. Other signals are chemical (pheromones), aural (sound), visual (courtship and aggressive displays), or tactile (touch). These types of communication may be instinctual or learned or a combination of both. These are not the same as the communication we associate with language, which has been observed only in humans and perhaps in some species of primates and cetaceans.

A pheromone is a secreted chemical signal used to obtain a response from another individual of the same species. The purpose of pheromones is to elicit a specific behavior from the receiving individual. Pheromones are especially common among social insects, but they are used by many species to attract the opposite sex, to sound alarms, to mark food trails, and to elicit other, more complex behaviors. Even humans are thought to respond to certain pheromones called axillary steroids. These chemicals influence human perception of other people,

and in one study were responsible for a group of people synchronizing their menstrual cycles. The role of pheromones in human-to-human communication is not fully understood and continues to be researched.

Songs are an example of an aural signal, one that needs to be heard by the recipient. Perhaps the best known of these are songs of birds, which identify the species and are used to attract mates. Other well-known songs are those of whales, which are of such low frequency that they can travel long distances underwater. Dolphin species communicate with each other (and occasionally even with other species of dolphins) using a wide variety of vocalizations. Male crickets make chirping sounds using a specialized organ to attract a mate, repel other males, and to announce a successful mating.

Courtship displays are a series of ritualized visual behaviors (signals) designed to attract and convince a member of the opposite sex to mate. These displays are ubiquitous in the animal kingdom. Often these displays involve a series of steps, including an initial display by one member followed by a response from the other. If at any point, the display is performed incorrectly or a proper response is not given, the mating ritual is abandoned and the mating attempt will be unsuccessful. The mating display of the common stork is shown in Figure 45.37.

Aggressive displays are also common in the animal kingdom. For example, a dog bares its teeth when it wants another dog to back down. Presumably, these displays communicate not only the willingness of the animal to fight, but also its fighting ability. Although these displays do signal aggression on the part of the sender, it is thought that these displays are actually a mechanism to reduce the amount of actual fighting that occurs between members of the same species: they allow individuals to assess the fighting ability of their opponent and thus decide whether it is "worth the fight." The testing of certain hypotheses using game theory has led to the conclusion that some of these displays may overstate an animal's actual fighting ability and are used to "bluff" the opponent. This type of interaction, even if "dishonest," would be favored by natural selection if it is successful more times than not.



Figure 45.37 This stork's courtship display is designed to attract potential mates. (credit: Linda "jinterwas"/Flickr)

Distraction displays are seen in birds and some fish. They are designed to attract a predator away from the nest. This is an example of an altruistic behavior: it benefits the young more than the individual performing the display, which is putting itself at risk by doing so.

Many animals, especially primates, communicate with other members in the group through touch. Activities such as grooming, touching the shoulder or root of the tail, embracing, lip contact, and greeting ceremonies have all been observed in the Indian langur, an Old World monkey. Similar behaviors are found in other primates, especially in the great apes.

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The killdeer bird distracts predators from its eggs by faking a broken wing display in this video taken in Boise, Idaho.

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ALTRUISTIC BEHAVIORS

Behaviors that lower the fitness of the individual but increase the fitness of another individual are termed altruistic. Examples of such behaviors are seen widely across the animal kingdom. Social insects such as worker bees have no ability to reproduce, yet they maintain the queen so she can populate the hive with her offspring. Meerkats keep a sentry standing guard to warn the rest of the colony about intruders, even though the sentry is putting itself at risk. Wolves and wild dogs bring meat to pack members not present during a hunt. Lemurs take care of infants unrelated to them. Although on the surface, these behaviors appear to be altruistic, the truth may not be so simple.

There has been much discussion over why altruistic behaviors exist. Do these behaviors lead to overall evolutionary advantages for their species? Do they help the altruistic individual pass on its own genes? And what about such activities between unrelated individuals? One explanation for altruistic-type behaviors is found in the genetics of natural selection. In the 1976 book, *The Selfish Gene*, scientist Richard Dawkins attempted to explain many seemingly altruistic behaviors from the viewpoint of the gene itself. Although a gene obviously cannot be selfish in the human sense, it may appear that way if the sacrifice of an individual benefits related individuals that share genes that are identical by descent (present in relatives because of common lineage). Mammal parents make this sacrifice to take care of their offspring. Emperor penguins migrate miles in harsh conditions to bring food back for their young. Selfish gene theory has been controversial over the years and is still discussed among scientists in related fields.

Even less-related individuals, those with less genetic identity than that shared by parent and offspring, benefit from seemingly altruistic behavior. The activities of social insects such as bees, wasps, ants, and termites are good examples. Sterile workers in these societies take care of the queen because they are closely related to it, and as the queen has offspring, she is passing on genes from the workers indirectly. Thus, it is of fitness benefit for the worker to maintain the queen without having any direct chance of passing on its genes due to its sterility. The lowering of individual fitness to enhance the reproductive fitness of a relative and thus one's inclusive fitness evolves through kin selection. This phenomenon can explain many superficially altruistic behaviors seen in animals. However, these behaviors may not be truly defined as altruism in these cases because the actor is actually increasing its own fitness either directly (through its own offspring) or indirectly (through the inclusive fitness it gains through relatives that share genes with it).

Unrelated individuals may also act altruistically to each other, and this seems to defy the "selfish gene" explanation. An example of this observed in many monkey species where a monkey will present its back to an unrelated monkey to have that individual pick the parasites from its fur. After a certain amount of time, the roles are reversed and the first monkey now grooms the second monkey. Thus, there is reciprocity in the behavior. Both benefit from the interaction and their fitness is raised more than if neither cooperated nor if one cooperated and the other did not cooperate. This behavior is still not necessarily altruism, as the "giving" behavior of the actor is based on the expectation that it will be the "receiver" of the behavior in the future, termed reciprocal altruism. Reciprocal altruism requires that

individuals repeatedly encounter each other, often the result of living in the same social group, and that cheaters (those that never "give back") are punished.

Evolutionary game theory, a modification of classical game theory in mathematics, has shown that many of these so-called "altruistic behaviors" are not altruistic at all. The definition of "pure" altruism, based on human behavior, is an action that benefits another without any direct benefit to oneself. Most of the behaviors previously described do not seem to satisfy this definition, and game theorists are good at finding "selfish" components in them. Others have argued that the terms "selfish" and "altruistic" should be dropped completely when discussing animal behavior, as they describe human behavior and may not be directly applicable to instinctual animal activity. What is clear, though, is that heritable behaviors that improve the chances of passing on one's genes or a portion of one's genes are favored by natural selection and will be retained in future generations as long as those behaviors convey a fitness advantage. These instinctual behaviors may then be applied, in special circumstances, to other species, as long as it doesn't lower the animal's fitness.

FINDING SEX PARTNERS

Not all animals reproduce sexually, but many that do have the same challenge: they need to find a suitable mate and often have to compete with other individuals to obtain one. Significant energy is spent in the process of locating, attracting, and mating with the sex partner. Two types of selection occur during this process: intersexual selection, where individuals of one sex choose mates of the other sex, and intrasexual selection, the competition for mates between species members of the same sex. Intersexual selection is often complex because choosing a mate may be based on a variety of visual, aural, tactile, and chemical cues. An example of intersexual selection is when female peacocks choose to mate with the male with the brightest plumage. This type of selection often leads to traits in the chosen sex that do not enhance survival, but are those traits most attractive to the opposite sex (often at the expense of survival). Intrasexual selection involves mating displays and aggressive mating rituals such as rams butting heads—the winner of these battles is the one that is able to mate. Many of these rituals use up considerable energy but result in the selection of the healthiest, strongest, and/or most dominant individuals for mating.

Three general mating systems, all involving innate as opposed to learned behaviors, are seen in animal populations: monogamous, polygynous, and polyandrous.

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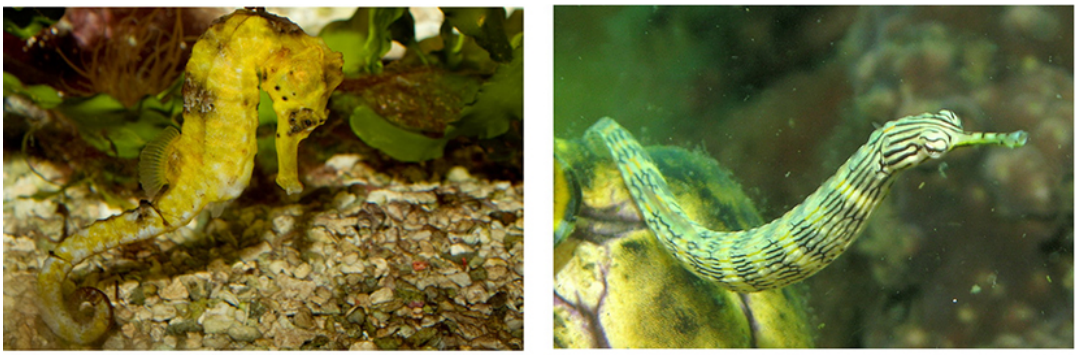
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Visit this website for informative videos on sexual selection.

In monogamous systems, one male and one female are paired for at least one breeding season. In some animals, such as the gray wolf, these associations can last much longer, even a lifetime. Several theories may explain this type of mating system. The "mate-guarding hypothesis" states that males stay with the female to prevent other males from mating with her. This behavior is advantageous in such situations where mates are scarce and difficult to find. Another explanation is the "male-assistance hypothesis," where males that help guard and rear their young will have more and healthier offspring. Monogamy is observed in many bird populations where, in addition to the parental care from the female, the male is also a major provider of parental care for the chicks. A third explanation for the evolutionary advantages of monogamy is the "female-enforcement hypothesis." In this scenario, the female ensures that the male does not have other offspring that might compete with her own, so she actively interferes with the male's signaling to attract other mates.

Polygynous mating refers to one male mating with multiple females. In these situations, the female must be responsible for most of the parental care as the single male is not capable of providing care to that many offspring. In resourced-based polygyny, males compete for territories with the best resources, and then mate with females that enter the territory, drawn to its resource richness. The female benefits by mating with a dominant, genetically fit male; however, it is at the cost of having no male help in caring for the offspring. An example is seen in the yellow-rumped honeyguide, a bird whose males defend beehives because the females feed on their wax. As the females approach, the male defending the nest will mate with them. Harem mating structures are a type of polygynous system where certain males dominate mating while controlling a territory with resources. Harem mating occurs in elephant seals, where the alpha male dominates the mating within the group. A third type of polygyny is a lek system. Here there is a communal courting area where several males perform elaborate displays for females, and the females choose their mate from this group. This behavior is observed in several bird species including the sage grouse and the prairie chicken.

In polyandrous mating systems, one female mates with many males. These types of systems are much rarer than monogamous and polygynous mating systems. In pipefishes and seahorses, males receive the eggs from the female, fertilize them, protect them within a pouch, and give birth to the offspring (Figure 45.38). Therefore, the female is able to provide eggs to several males without the burden of carrying the fertilized eggs.



(a) (b)

Figure 45.38 Polyandrous mating, in which one female mates with many males, occurs in the (a) seahorse and the (b) pipefish. (credit a: modification of work by Brian Gratwicke; credit b: modification of work by Stephen Childs)

SIMPLE LEARNED BEHAVIORS

The majority of the behaviors previously discussed were innate or at least have an innate component (variations on the innate behaviors may be learned). They are inherited and the behaviors do not change in response to signals from the environment. Conversely, learned behaviors, even though they may have instinctive components, allow an organism to adapt to changes in the environment and are modified by previous experiences. Simple learned behaviors include habituation and imprinting—both are important to the maturation process of young animals.

HABITUATION

Habituation is a simple form of learning in which an animal stops responding to a stimulus after a period of repeated exposure. This is a form of non-associative learning, as the stimulus is not associated with any punishment or reward. Prairie dogs typically sound an alarm call when threatened by a predator, but they become habituated to the sound of human footsteps when no harm is associated with this sound, therefore, they no longer respond to them with an alarm call. In this example, habituation is specific to the sound of human footsteps, as the animals still respond to the sounds of potential predators.

IMPRINTING

Imprinting is a type of learning that occurs at a particular age or a life stage that is rapid and independent of the species involved. Hatchling ducks recognize the first adult they see, their mother, and make a bond with her. A familiar sight is ducklings walking or swimming after their mothers (Figure 45.39). This is another type of non-associative learning, but is very important in the maturation process of these animals as it encourages them to stay near their mother so they will be protected, greatly increasing their chances of survival. However, if newborn ducks see a human before they see their mother, they will imprint on the human and follow it in just the same manner as they would follow their real mother.



Figure 45.39 The attachment of ducklings to their mother is an example of imprinting. (credit: modification of work by Mark Harkin)

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The International Crane Foundation has helped raise the world's population of whooping cranes from 21 individuals to about 600. Imprinting hatchlings has been a key to success: biologists wear full crane costumes so the birds never "see" humans. Watch this video to learn more.

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CONDITIONED BEHAVIOR

Conditioned behaviors are types of associative learning, where a stimulus becomes associated with a consequence. During operant conditioning, the behavioral response is modified by its consequences, with regards to its form, strength, or frequency.

CLASSICAL CONDITIONING

In classical conditioning, a response called the conditioned response is associated with a stimulus that it had previously not been associated with, the conditioned stimulus. The response to the original, unconditioned stimulus is called the unconditioned response. The most cited example of classical conditioning is Ivan Pavlov's experiments with dogs (Figure 45.40). In Pavlov's experiments, the unconditioned response was the salivation of dogs in response to the unconditioned stimulus of seeing or smelling their food. The conditioning stimulus that researchers associated with the unconditioned response was the ringing of a bell. During conditioning, every time the animal was given food, the bell was rung. This was repeated during several trials. After some time, the dog learned to associate the ringing of the bell with food and to respond by salivating. After the conditioning period was finished, the dog would respond by salivating when the bell was rung, even when the unconditioned stimulus, the food, was absent. Thus, the ringing of the bell became the conditioned stimulus and the salivation became the conditioned response. Although it is thought by some scientists that the unconditioned and conditioned responses are identical, even Pavlov discovered that the saliva in the conditioned dogs had characteristic differences when compared to the unconditioned dog.



Figure 45.40 In the classic Pavlovian response, the dog becomes conditioned to associate the ringing of the bell with food.

It had been thought by some scientists that this type of conditioning required multiple exposures to the paired stimulus and response, but it is now known that this is not necessary in all cases, and that some conditioning can be learned in a single pairing experiment. Classical conditioning is a major tenet of behaviorism, a branch of psychological philosophy that proposes that all actions, thoughts, and emotions of living things are behaviors that can be treated by behavior modification and changes in the environment.

OPERANT CONDITIONING

In operant conditioning, the conditioned behavior is gradually modified by its consequences as the animal responds to the stimulus. A major proponent of such conditioning was psychologist B.F. Skinner, the inventor of the Skinner box. Skinner put rats in his boxes that contained a lever that would dispense food to the rat when depressed. While initially the rat would push the lever a few times by accident, it eventually associated pushing the lever with getting the food. This type of learning is an example of operant conditioning. Operant learning is the basis of most animal training. The conditioned behavior is continually modified by positive or negative reinforcement, often a reward such as food or some type of punishment, respectively. In this way, the animal is conditioned to associate a type of behavior with the punishment or reward, and, over time, can be induced to perform behaviors that they would not have done in the wild, such as the “tricks” dolphins perform at marine amusement park shows (Figure 45.41).



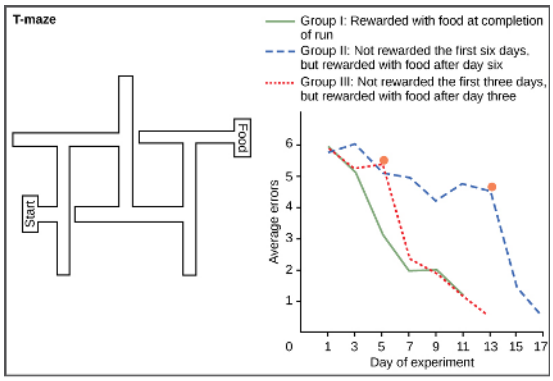
Figure 45.41 The training of dolphins by rewarding them with food is an example of positive reinforcement operant conditioning. (credit: Roland Tanglao)

COGNITIVE LEARNING

Classical and operant conditioning are inefficient ways for humans and other intelligent animals to learn. Some primates, including humans, are able to learn by imitating the behavior of others and by taking instructions. The development of complex language by humans has made cognitive learning, the manipulation of information using the mind, the most prominent method of human learning. In fact, that is how students are learning right now by reading this book. As students read, they can make mental images of objects or organisms and imagine changes to them, or behaviors by them, and anticipate the consequences. In addition to visual processing, cognitive learning is also enhanced by remembering past experiences, touching physical objects, hearing sounds, tasting food, and a variety of other sensory-based inputs. Cognitive learning is so powerful that it can be used to understand conditioning in detail. In the reverse scenario, conditioning cannot help someone learn about cognition.

Classic work on cognitive learning was done by Wolfgang Köhler with chimpanzees. He demonstrated that these animals were capable of abstract thought by showing that they could learn how to solve a puzzle. When a banana was hung in their cage too high for them to reach, and several boxes were placed randomly on the floor, some of the chimps were able to stack the boxes one on top of the other, climb on top of them, and get the banana. This implies that they could visualize the result of stacking the boxes even before they had performed the action. This type of learning is much more powerful and versatile than conditioning.

Cognitive learning is not limited to primates, although they are the most efficient in using it. Maze running experiments done with rats by H.C. Blodgett in the 1920s were the first to show cognitive skills in a simple mammal. The motivation for the animals to work their way through the maze was a piece of food at its end. In these studies, the animals in Group I were run in one trial per day and had food available to them each day on completion of the run (Figure 45.42). Group II rats were not fed in the maze for the first six days and then subsequent runs were done with food for several days after. Group III rats had food available on the third day and every day thereafter. The results were that the control rats, Group I, learned quickly, and figured out how to run the maze in seven days. Group III did not learn much during the three days without food, but rapidly caught up to the control group when given the food reward. Group II learned very slowly for the six days with no reward to motivate them, and they did not begin to catch up to the control group until the day food was given, and then it took two days longer to learn the maze.



Redrawn after H. C. Blodgett, The effect of the introduction of reward upon the maze performance of rats. Univ. Calif. Publ. Psychol., 1929, 4, No. 8, pages 117 and 120.

Figure 45.42 Group I (the green solid line) found food at the end of each trial, group II (the blue dashed line) did not find food for the first 6 days, and group III (the red dotted line) did not find food during runs on the first three days. Notice that rats given food earlier learned faster and eventually caught up to the control group. The orange dots on the group II and III lines show the days when food rewards were added to the mazes.

It may not be immediately obvious that this type of learning is different than conditioning. Although one might be tempted to believe that the rats simply learned how to find their way through a conditioned series of right and left turns, E.C. Tolman proved a decade later that the rats were making a representation of the maze in their minds, which he called a "cognitive map." This was an early demonstration of the power of cognitive learning and how these abilities were not just limited to humans.

SOCIOBIOLOGY

Sociobiology is an interdisciplinary science originally popularized by social insect researcher E.O. Wilson in the 1970s. Wilson defined the science as "the extension of population biology and evolutionary theory to social organization."[9]The main thrust of sociobiology is that animal and human behavior, including aggressiveness and other social interactions, can be explained almost solely in terms of genetics and natural selection. This science is controversial; noted scientists such as the late Stephen Jay Gould criticized the approach for ignoring the environmental effects on behavior. This is another example of the "nature versus nurture" debate of the role of genetics versus the role of environment in determining an organism's characteristics.

Sociobiology also links genes with behaviors and has been associated with "biological determinism," the belief that all behaviors are hardwired into our genes. No one disputes that certain behaviors can be inherited and that natural selection plays a role retaining them. It is the application of such principles to human behavior that sparks this controversy, which remains active today.

FOOTNOTES

- 9Edward O. Wilson. *On Human Nature* (1978; repr., Cambridge: Harvard University Press, 2004), xx.

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CHAPTER OVERVIEW

7: ECOSYSTEMS

Ecosystem ecology is the integrated study of living (biotic) and non-living (abiotic) components of ecosystems and their interactions within an ecosystem framework. This science examines how ecosystems work and relates this to their components such as chemicals, bedrock, soil, plants, and animals.

7.1: Introduction

7.2: Ecology of Ecosystems

7.2.1: Ecosystems

7.3: Energy Flow through Ecosystems

7.3.1: Energy in Ecosystems

7.4: Biogeochemical Cycles

7.4.1: Biogeochemical Cycles

7.5: Soils

7.5.1: Soil Degradation

7.6: Key Terms

7.7: Chapter Summary

7.8: Visual Connection Questions

7.9: Review Questions

7.10: Critical Thinking Questions

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7.1: INTRODUCTION



Figure 46.1 In the southwestern United States, rainy weather causes an increase in production of pinyon nuts, causing the deer mouse population to explode. Deer mice may carry a virus called *Sin Nombre* (a hantavirus) that causes respiratory disease in humans and has a high fatality rate. In 1992–1993, wet *El Niño* weather caused a *Sin Nombre* epidemic. Navajo healers, who were aware of the link between this disease and weather, predicted the outbreak. (credit "highway": modification of work by Phillip Capper; credit "mouse": modification of work by USFWS)

CHAPTER OUTLINE

46.1 Ecology of Ecosystems
46.2 Energy Flow through Ecosystems
46.3 Biogeochemical Cycles

In 1993, an interesting example of ecosystem dynamics occurred when a rare lung disease struck inhabitants of the southwestern United States. This disease had an alarming rate of fatalities, killing more than half of early patients, many of whom were Native Americans. These formerly healthy young adults died from complete respiratory failure. The disease was unknown, and the Centers for Disease Control (CDC), the United States government agency responsible for managing potential epidemics, was brought in to investigate. The scientists could have learned about the disease had they known to talk with the Navajo healers who lived in the area and who had observed the connection between rainfall and mice populations, thereby predicting the 1993 outbreak.

The cause of the disease, determined within a few weeks by the CDC investigators, was the hantavirus known as *Sin Nombre*, the virus with “no name.” With insights from traditional Navajo medicine, scientists were able to characterize the disease rapidly and institute effective health measures to prevent its spread. This example illustrates the importance of understanding the complexities of ecosystems and how they respond to changes in the environment.

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7.2: ECOLOGY OF ECOSYSTEMS

LEARNING OBJECTIVES

By the end of this section, you will be able to do the following:

- Describe the basic ecosystem types
- Explain the methods that ecologists use to study ecosystem structure and dynamics
- Identify the different methods of ecosystem modeling
- Differentiate between food chains and food webs and recognize the importance of each

Life in an ecosystem is often about competition for limited resources, a characteristic of the theory of natural selection. Competition in communities (all living things within specific habitats) is observed both within species and among different species. The resources for which organisms compete include organic material, sunlight, and mineral nutrients, which provide the energy for living processes and the matter to make up organisms' physical structures. Other critical factors influencing community dynamics are the components of its physical and geographic environment: a habitat's latitude, amount of rainfall, topography (elevation), and available species. These are all important environmental variables that determine which organisms can exist within a particular area.

An ecosystem is a community of living organisms and their interactions with their abiotic (nonliving) environment. Ecosystems can be small, such as the tide pools found near the rocky shores of many oceans, or large, such as the Amazon Rainforest in Brazil (Figure 46.2).

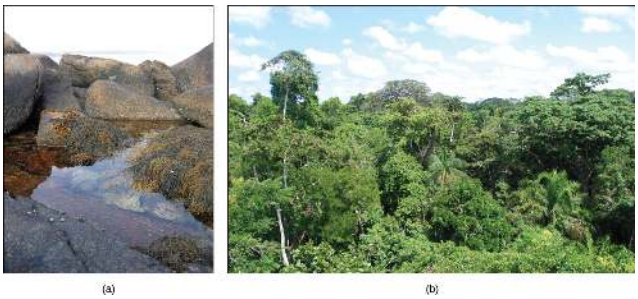


Figure 46.2 A (a) tidal pool ecosystem in Matinicus Island in Maine is a small ecosystem, while the (b) Amazon Rainforest in Brazil is a large ecosystem. (credit a: modification of work by "takomabibelot"/Flickr; credit b: modification of work by Ivan Mlinaric)

There are three broad categories of ecosystems based on their general environment: freshwater, ocean water, and terrestrial. Within these broad categories are individual ecosystem types based on the organisms present and the type of environmental habitat.

Ocean ecosystems are the most common, comprising over 70 percent of the Earth's surface and consisting of three basic types: shallow ocean, deep ocean water, and deep ocean surfaces (the low depth areas of the deep oceans). The shallow ocean ecosystems include extremely biodiverse coral reef ecosystems, and the deep ocean surface is known for its large numbers of plankton and krill (small crustaceans) that support it. These two environments are especially important to aerobic respirators worldwide as the phytoplankton perform 40 percent of all photosynthesis on Earth. Although not as diverse as the other two, deep ocean ecosystems contain a wide variety of marine organisms. Such ecosystems exist even at the bottom of the ocean where light is unable to penetrate through the water.

Freshwater ecosystems are the rarest, occurring on only 1.8 percent of the Earth's surface. Lakes, rivers, streams, and springs comprise these systems. They are quite diverse, and they support a variety of fish, amphibians, reptiles, insects, phytoplankton, fungi, and bacteria.

Terrestrial ecosystems, also known for their diversity, are grouped into large categories called biomes, such as tropical rain forests, savannas, deserts, coniferous forests, deciduous forests, and tundra. Grouping these ecosystems into just a few biome categories obscures the great diversity of the individual ecosystems within them. For example, there is great variation in desert vegetation: the saguaro cacti and other plant life in the Sonoran Desert, in the United States, are relatively abundant compared to the desolate rocky desert of Boa Vista, an island off the coast of Western Africa (Figure 46.3).



Figure 46.3 Desert ecosystems, like all ecosystems, can vary greatly. The desert in (a) Saguaro National Park, Arizona, has abundant plant life, while the rocky desert of (b) Boa Vista island, Cape Verde, Africa, is devoid of plant life. (credit a: modification of work by Jay Galvin; credit b: modification of work by Ingo Wölbern)

Ecosystems are complex with many interacting parts. They are routinely exposed to various disturbances, or changes in the environment that effect their compositions: yearly variations in rainfall and temperature and the slower processes of plant growth, which may take several years. Many of these disturbances result from natural processes. For example, when lightning causes a forest fire and destroys part of a forest ecosystem, the ground is eventually populated by grasses, then by bushes and shrubs, and later by mature trees, restoring the forest to its former state. The impact of environmental disturbances caused by human activities is as important as the changes wrought by natural processes. Human agricultural practices, air pollution, acid rain, global deforestation, overfishing, eutrophication, oil spills, and waste dumping on land and into the ocean are all issues of concern to conservationists.

Equilibrium is the steady state of an ecosystem where all organisms are in balance with their environment and with each other. In ecology, two parameters are used to measure changes in ecosystems: resistance and resilience. Resistance is the ability of an ecosystem to remain at equilibrium in spite of disturbances. Resilience is the speed at which an ecosystem recovers equilibrium after being disturbed. Ecosystem resistance and resilience are especially important when considering human impact. The nature of an ecosystem may change to such a degree that it can lose its resilience entirely. This process can lead to the complete destruction or irreversible altering of the ecosystem.

FOOD CHAINS AND FOOD WEBS

The term “food chain” is sometimes used metaphorically to describe human social situations. Individuals who are considered successful are seen as being at the top of the food chain, consuming all others for their benefit, whereas the less successful are seen as being at the bottom.

The scientific understanding of a food chain is more precise than in its everyday usage. 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. Each organism in a food chain occupies what is called a trophic level. Depending on their role as producers or consumers, species or groups of species can be assigned to various trophic levels.

In many ecosystems, the bottom of the food chain consists of photosynthetic organisms (plants and/or phytoplankton), which are called primary producers. The organisms that consume the primary producers are herbivores: the primary consumers. Secondary consumers are usually carnivores that eat the primary consumers. Tertiary consumers are carnivores that eat other carnivores. Higher-level consumers feed on the next lower trophic levels, and so on, up to the organisms at the top of the food chain: the apex consumers. In the Lake Ontario food chain shown in Figure 46.4, the Chinook salmon is the apex consumer at the top of this food chain.

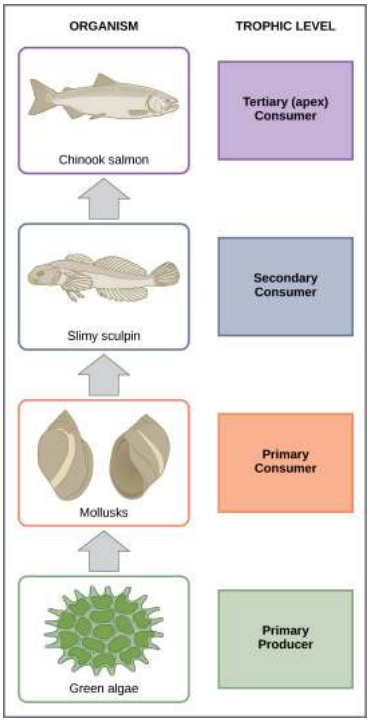


Figure 46.4 These are the trophic levels of a food chain in Lake Ontario at the United States-Canada border. Energy and nutrients flow from photosynthetic green algae at the bottom to the top of the food chain: the Chinook salmon.

One major factor that limits the length of food chains is energy. Energy is lost as heat between each trophic level due to the second law of thermodynamics. Thus, after a limited number of trophic energy transfers, the amount of energy remaining in the food chain may not be great enough to support viable populations at yet a higher trophic level.

The loss of energy between trophic levels is illustrated by the pioneering studies of Howard T. Odum in the Silver Springs, Florida, ecosystem in the 1940s (Figure 46.5). The primary producers generated 20,819 kcal/m^2/yr (kilocalories per square meter per year), the primary consumers generated 3368 kcal/m^2/yr, the secondary consumers generated 383 kcal/m^2/yr, and the tertiary consumers only generated 21 kcal/m^2/yr. Thus, there is little energy remaining for another level of consumers in this ecosystem.

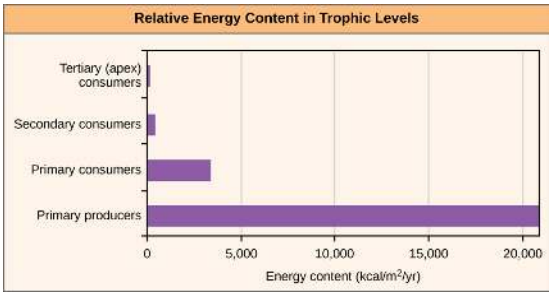


Figure 46.5 The relative energy in trophic levels in a Silver Springs, Florida, ecosystem is shown. Each trophic level has less energy available and supports fewer organisms at the next level.

There is a one problem when using food chains to 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 46.6).

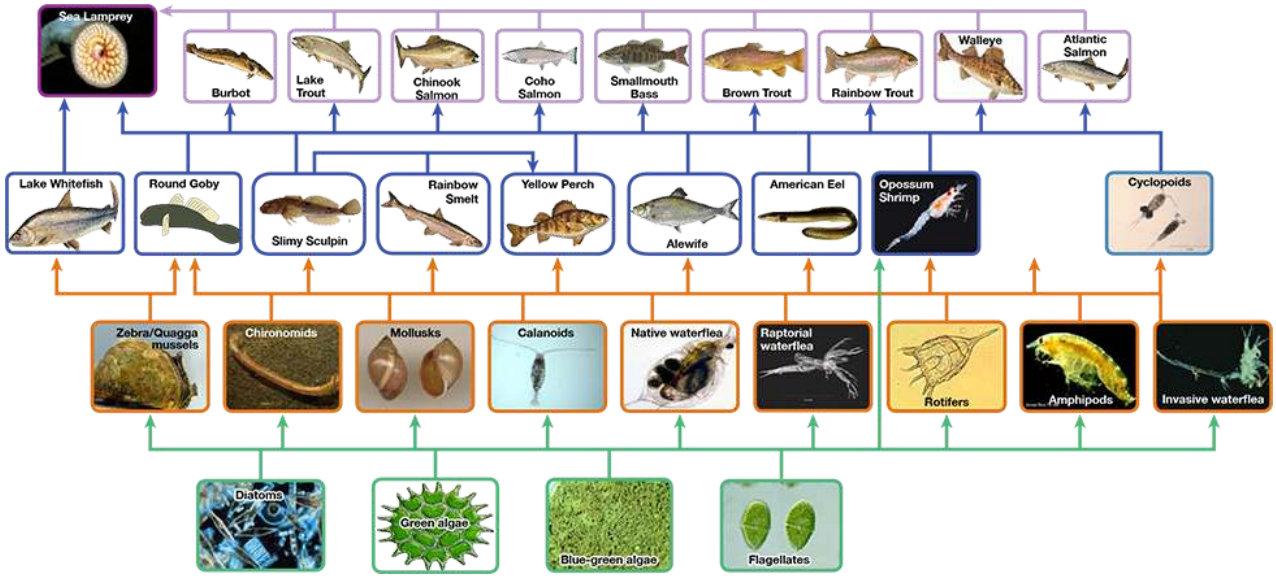


Figure 46.6 This food web shows the interactions between organisms across trophic levels in the Lake Ontario ecosystem. Primary producers are outlined in green, primary consumers in orange, secondary consumers in blue, and tertiary (apex) consumers in purple. Arrows point from an organism that is consumed to the organism that consumes it. Notice how some lines point to more than one trophic level. For example, the opossum shrimp eats both primary producers and primary consumers. (credit: NOAA, GLERL)

A comparison of the two types of structural ecosystem models shows strength in both. Food chains are more flexible for analytical modeling, are easier to follow, and are easier to experiment with, whereas food web models more accurately represent ecosystem structure and dynamics, and data can be directly used as input for simulation modeling.

LINK TO LEARNING

LINK TO LEARNING

Head to this online interactive simulator to investigate food web function. In the *Interactive Labs* box, under Food Web, click **Step 1**. Read the instructions first, and then click **Step 2** for additional instructions. When you are ready to create a simulation, in the upper-right corner of the *Interactive Labs* box, click **OPEN SIMULATOR**.

Two general types of food webs are often shown interacting within a single ecosystem. A grazing food web (such as the Lake Ontario food web in Figure 46.6) has plants or other photosynthetic organisms at its base, followed by herbivores and various carnivores. A detrital food web consists of a base of organisms that feed on decaying organic matter (dead organisms), called decomposers or detritivores. These organisms are usually bacteria or fungi that recycle organic material back into the biotic part of the ecosystem as they themselves are consumed by other organisms. As all ecosystems require a method to recycle material from dead organisms, most grazing food webs have an associated detrital food web. For example, in a meadow ecosystem, plants may support a grazing food web of different organisms, primary and other levels of consumers, while at the same time supporting a detrital food web of bacteria, fungi, and detrivorous invertebrates feeding off dead plants and animals.

EVOLUTION CONNECTION

EVOLUTION CONNECTION

Three-spined SticklebackIt is well established by the theory of natural selection that changes in the environment play a major role in the evolution of species within an ecosystem. However, little is known about how the evolution of species within an ecosystem can alter the ecosystem environment. In 2009, Dr. Luke Harmon, from the University of Idaho, published a paper that for the first time showed that the evolution of organisms into subspecies can have direct effects on their ecosystem environment.[1]

The three-spined stickleback (*Gasterosteus aculeatus*) is a freshwater fish that evolved from a saltwater fish to live in freshwater lakes about 10,000 years ago, which is considered a recent development in evolutionary time (Figure 46.7). Over the last 10,000 years, these freshwater fish then became isolated from each other in different lakes. Depending on which lake population was studied, findings showed that these sticklebacks then either remained as one species or evolved into two species. The divergence of species was made possible by their use of different areas of the pond for feeding called micro niches.

Dr. Harmon and his team created artificial pond microcosms in 250-gallon tanks and added muck from freshwater ponds as a source of zooplankton and other invertebrates to sustain the fish. In different experimental tanks they introduced one species of stickleback from either a single-species or double-species lake.

Over time, the team observed that some of the tanks bloomed with algae while others did not. This puzzled the scientists, and they decided to measure the water's dissolved organic carbon (DOC), which consists of mostly large molecules of decaying organic matter that give pond-water its slightly brownish color. It turned out that the water from the tanks with two-species fish contained larger particles of DOC (and hence darker water) than water with single-species fish. This increase in DOC blocked the sunlight and prevented algal blooming. Conversely, the water from the single-species tank contained smaller DOC particles, allowing more sunlight penetration to fuel the algal blooms.

This change in the environment, which is due to the different feeding habits of the stickleback species in each lake type, probably has a great impact on the survival of other species in these ecosystems, especially other photosynthetic organisms. Thus, the study shows that, at least in these ecosystems, the environment and the evolution of populations have reciprocal effects that may now be factored into simulation models.



Figure 46.7 The three-spined stickleback evolved from a saltwater fish to freshwater fish. (credit: Barrett Paul, USFWS)

RESEARCH INTO ECOSYSTEM DYNAMICS: ECOSYSTEM EXPERIMENTATION AND MODELING

The study of the changes in ecosystem structure caused by changes in the environment (disturbances) or by internal forces is called ecosystem dynamics. Ecosystems are characterized using a variety of research methodologies. Some ecologists study ecosystems using controlled experimental systems, while some study entire ecosystems in their natural state, and others use both approaches.

A holistic ecosystem model attempts to quantify the composition, interaction, and dynamics of entire ecosystems; it is the most representative of the ecosystem in its natural state. A food web is an example of a holistic ecosystem model. However, this type of study is limited by time and expense, as well as the fact that it is neither feasible nor ethical to do experiments on large natural ecosystems. It is difficult to quantify all different species in an ecosystem and the dynamics in their habitat, especially when studying large habitats such as the Amazon Rainforest.

For these reasons, scientists study ecosystems under more controlled conditions. Experimental systems usually involve either partitioning a part of a natural ecosystem that can be used for experiments, termed a mesocosm, or by recreating an ecosystem entirely in an indoor or outdoor laboratory environment, which is referred to as a microcosm. A major limitation to these approaches is that removing individual organisms from their natural ecosystem or altering a natural ecosystem through partitioning may change the dynamics of the ecosystem. These changes are often due to differences in species numbers and diversity and also to environment alterations caused by partitioning (mesocosm) or recreating (microcosm) the natural habitat. Thus, these types of experiments are not totally predictive of changes that would occur in the ecosystem from which they were gathered.

As both of these approaches have their limitations, some ecologists suggest that results from these experimental systems should be used only in conjunction with holistic ecosystem studies to obtain the most representative data about ecosystem structure, function, and dynamics.

Scientists use the data generated by these experimental studies to develop ecosystem models that demonstrate the structure and dynamics of ecosystems. They use three basic types of ecosystem modeling in research and ecosystem management: a conceptual model, an analytical model, and a simulation model. A conceptual model is an ecosystem model that consists of flow charts to show interactions of different compartments of the living and nonliving components of the ecosystem. A conceptual model describes ecosystem structure and dynamics and shows how environmental disturbances affect the ecosystem; however, its ability to predict the effects of these disturbances is limited. Analytical and simulation models, in contrast, are mathematical methods of describing ecosystems that are indeed capable of predicting the effects of potential environmental changes without direct experimentation, although with some limitations as to accuracy. An analytical model is an ecosystem model that is created using simple mathematical formulas to predict the effects of environmental disturbances on ecosystem structure and dynamics. A simulation model is an ecosystem model that is created using complex computer algorithms to holistically model ecosystems and to predict the effects of environmental disturbances on ecosystem structure and dynamics. Ideally, these models are accurate enough to determine which components of the ecosystem are particularly sensitive to disturbances, and they can serve as a guide to ecosystem managers (such as conservation ecologists or fisheries biologists) in the practical maintenance of ecosystem health.

CONCEPTUAL MODELS

Conceptual models are useful for describing ecosystem structure and dynamics and for demonstrating the relationships between different organisms in a community and their environment. Conceptual models are usually depicted graphically as flow charts. The organisms and their resources are grouped into specific compartments with arrows showing the relationship and transfer of energy or nutrients between them. Thus, these diagrams are sometimes called compartment models.

To model the cycling of mineral nutrients, organic and inorganic nutrients are subdivided into those that are bioavailable (ready to be incorporated into biological macromolecules) and those that are not. For example, in a terrestrial ecosystem near a deposit of coal, carbon will be available to the plants of this ecosystem as carbon dioxide gas in a short-term period, not from the carbon-rich coal itself. However, over a longer period, microorganisms capable of digesting coal will incorporate its carbon or release it as natural gas (methane, CH_4), changing this unavailable organic source into an available one. This conversion is greatly accelerated by the combustion of fossil fuels by humans, which releases large amounts of carbon dioxide into the atmosphere. This is thought to be a major factor in the rise of the atmospheric carbon dioxide levels in the industrial age. The carbon dioxide released from burning fossil fuels is produced faster than photosynthetic organisms can use it. This process is intensified by the reduction of photosynthetic trees because of worldwide deforestation. Most scientists agree that high atmospheric carbon dioxide is a major cause of global climate change.

Conceptual models are also used to show the flow of energy through particular ecosystems. Figure 46.8 is based on Howard T. Odum's classical study of the Silver Springs, Florida, holistic ecosystem in the mid-twentieth century.[2] This study shows the energy content and transfer between various ecosystem compartments.

VISUAL CONNECTION

VISUAL CONNECTION

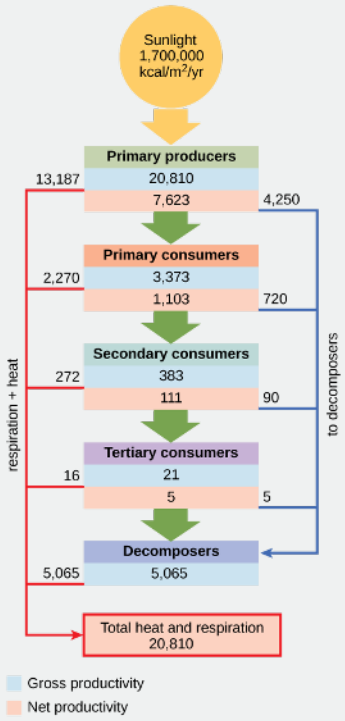


Figure 46.8 This conceptual model shows the flow of energy through a spring ecosystem in Silver Springs, Florida. Notice that the energy decreases with each increase in trophic level.

Why do you think the value for gross productivity of the primary producers is the same as the value for total heat and respiration (20,810 kcal/m^2/yr)?

ANALYTICAL AND SIMULATION MODELS

The major limitation of conceptual models is their inability to predict the consequences of changes in ecosystem species and/or environment. Ecosystems are dynamic entities and subject to a variety of abiotic and biotic disturbances caused by natural forces and/or human activity. Ecosystems altered from their initial equilibrium state can often recover from such disturbances and return to a state of equilibrium. As most ecosystems are subject to periodic disturbances and are often in a state of change, they are usually either moving toward or away from their equilibrium state. There are many of these equilibrium states among the various components of an ecosystem, which affects the ecosystem overall. Furthermore, as humans have the ability to greatly and rapidly alter the species content and habitat of an ecosystem, the need for predictive models that enable understanding of how ecosystems respond to these changes becomes more crucial.

Analytical models often use simple, linear components of ecosystems, such as food chains, and are known to be complex mathematically; therefore, they require a significant amount of mathematical knowledge and expertise. Although analytical models have great potential, their simplification of complex ecosystems is thought to limit their accuracy. Simulation models that use computer programs are better able to deal with the complexities of ecosystem structure.

A recent development in simulation modeling uses supercomputers to create and run individual-based simulations, which accounts for the behavior of individual organisms and their effects on the ecosystem as a whole. These simulations are considered to be the most accurate and predictive of the complex responses of ecosystems to disturbances.

LINK TO LEARNING

LINK TO LEARNING

Visit The Darwin Project to view a variety of ecosystem models, including simulations that model predator-prey relationships to learn more.

FOOTNOTES

- 1*Nature* (Vol. 458, April 1, 2009)
- 2Howard T. Odum, “Trophic Structure and Productivity of Silver Springs, Florida,” *Ecological Monographs* 27, no. 1 (1957): 47–112.

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SECTION OVERVIEW

7.2.1: Ecosystems

An ecosystem can be described simply as the collection of all living and non-living components in a particular area. The living components of the environment are known as biotic factors. Biotic factors include plants, animals, and micro-organisms. The non-living components of the environment are known as abiotic factors. Abiotic factors include things such as rocks,water,soil,light,etc.

The idea of the ecosystem relates to the idea that all organisms in the environment are engaged in relationships with every other aspect (like resources and other organisms) in that environment. Ecosystems deal with energy and nutrient flow through a system/community. For example, a household or a university could be described as an ecosystem, and a city or a state could be described as a larger ecosystem.

While ecosystems may be bound and individually discussed, they do not exist independently, but interact in a complex web. The ecological relationships connecting all ecosystems make up the biosphere. Because virtually no surface on the Earth is free of human contact, all ecosystems can be accurately classified as human ecosystems.

Ecosystems vary in diversity. Some ecosystems may be very diverse with many plants and animals; whereas other ecosystems may be less diverse with fewer animals and plants. For example, tropical rain forests could be classified as an ecosystem that has high diversity; whereas temperate rain forests could be classified as an ecosystem that has lower diversity as compared to tropical rain forests.



A tropical rain forest is an example of an ecosystem that may support several amounts of plants and animals and therefore may have a high diversity

Ecosystem Concept

> *Living organisms and their nonliving (abiotic) environment are inseparably interrelated and interact upon each other. Any area of nature that includes living organisms and non-living substances interacting to produce an exchange of materials between the living and non-living parts is an* ecological system *or* ***ecosystem*** - E. P. Odum, 1959 (emphasis added)



The Bald eagle *Haliaeetus leucocephalus* is a top predator; a consumer whose niche is at the top of the food web

Thus, a Field Mouse (say a Meadow vole, *Microtus pennsylvanicus*) in its burrow in the soil is interacting with the non-living elements of that burrow as it breathes, taking in oxygen and expelling carbon dioxide[1]. But that activity is but a moment in time and cannot, by itself, define an ecosystem. The mouse must leave the burrow for food, interacting with plants. Plants themselves interact and exchange materials with the soil and the atmosphere and are dependent on radiation from the sun and the activity of earthworms and fungi in the soil. The latter, in turn, feed upon organic molecules left behind from the death of former living plants (and field mice). Thus, the "ecosystem" of our field mouse includes plants, and soil, and soil organisms—and of course other field mice to insure that mice will always be a part of that ecosystem. And perhaps present are Bald eagles (*Haliaeetus leucocephalus*), dependent upon trees for nesting and roosting and a stream for water (and fish as an alternative food), feeding upon Field mice, recycling those that are caught into baby Bald eagles and droppings that are food for the plants and earthworms. Already, the "area" of this ecosystem is at least as large as that required to support a **population** of Bald eagles.

It is the inclusion of all the interrelationships within a functional system that make the concept of ecosystem so broad. And the seemingly endless networks of links and interactions that give geographical breadth to an ecosystem. Of course, an ecologist could study just the organisms, activities, and biotic/abiotic interactions within the local "soil ecosystem", treating mouse and eagle excrement as we described the sun above: external, but providing important input of energy and material to the soil ecosystem. In a sense, this is what we mean by calling "ecosystem" a concept rather than just a place. We may conceive of, for the purpose of study, ecosystems over a wide range of sizes or scale, from an aquarium to an ocean, and lots of places in between. Essential are certain components that we alluded to in our description of parts of the ecosystem supporting habitat for the Field mouse, and these we will next explore in detail.

In attempting to understand any interactive, complex system, especially one as elaborate as even a simple ecosystem, it is helpful to break the system down into various component parts. By this mental process we can arrive at some understanding of the specific system and can make comparisons with other systems to further our understanding of ecosystems in general. An ecosystem consists of many component structures and these function together in various ways, suggesting an initial approach to describe any ecosystem is to consider separately its structural and functional aspects.

Basic Structural Components

Consider first an ecosystem from a structural perspective: an ecosystem consists of living (biotic) and non-living (abiotic) components. Living components include populations of organisms and the living resources they use. Non-living components include non-living resources, such as space, and the non-living physical characteristics of habitats that differ by location, such as elevation, temperature, and humidity.

We know and can observe that the **organisms** living in almost any ecosystem are not all identical individuals, but can be categorized into species (discussed previously in Chapter 9); and each species has a unique set of morphological, physiological, and behavioral attributes (see Chapter 3) that will determine how each individual functions within the whole. The species present provide ways of considering their contribution to ecosystem structure. For examples: we could describe the number of species (species richness), or the number (or biomass) of individuals of each species (species diversity), or their distribution across the physical space of the ecosystem. These are a few ways an ecologist would approach describing ecosystem structure based upon the plants and animals (and others) present in it.

In addition to the organisms themselves, there are components utilized by the organisms that comprise the **resources** of the ecosystem. These are both biotic and abiotic, inorganic and organic, and are exchanged between organisms and between organisms and the environment (previously covered in part in Chapter 4). Resources are the materials cycled by the inhabitants of an ecosystem as they carry on with life processes. We say "cycled" because all living things have a finite existence, and the substances of their material composition remain after death to be utilized in other ways.

Finally, there are those factors that are the conditions under which the organisms live. The environment of a subarctic lake is vastly different from that of a forest in the wet tropics. But consider also that conditions within a pond (an aquatic environment) are very different from those just a few yards up from the shore (a terrestrial environment). While we might be describing mostly **physical conditions**, these need not be always abiotic. In many ecosystems there are organisms that provide or create the dominant physical structure of that ecosystem. Examples are a forest and a coral reef. In a forest ecosystem, the trees are both very prominent organisms and resources to many of the other species present; but they also have a substantial effect on the conditions—the microclimates—that prevail in the forest ecosystem by providing shade and physical structure for many other organisms that may not directly utilize the trees as a food resource.

It should be clear that when we speak of ecosystem structure, we are considering various aspects of an ecosystem from a perspective that need not—indeed does not—mesh exactly with other ways of categorizing ecosystem components. Consider the trees of a forest or the coral heads of a coral reef. Each is a living organism, a resource used by many other species, and a physical structure that determines the uniqueness of its particular ecosystem compared with the environment that would occupy the same space in the absence of either trees or corals. In describing ecosystem structure, we do not break down the components into divisions of abiotic vs. biotic, inorganic vs. organic, or by species. In the next section, we will consider components on the basis of their function in an ecosystem, creating yet another set of categories independent of the structural ones.

Characteristics of Ecosystems



An example of a marine ecosystem



Acheta domesticus organism that helps maintain its ecosystem

The complexity of an ecosystem will increase as the species diversity present in the ecosystem increases. Ecosystems that are not species rich (barren ecosystems) may *appear* to be physically complex but are actually considered *functionally* complex.

Even if few species live in an environment, often because it is an unfavorable environments, that ecosystem can be still functionally complex if it include species with remarkable biochemical specializations that allow them to survive. For instance some archaea live in environments that are 113-176° F. and some organisms can get energy from inorganic chemical sources, such as bacteria that break down crude oil.

A healthy ecosystem will have high species diversity and is not likely to be damaged by human interactions, natural disasters, and climate changes. Every species within an ecosystem has a *niche*, the unique way that a given species uses its environment. New species are discovered every day and the roles they play in their environment to keep it healthy. This idea behind the species within the environment using their niches to keep it healthy can clearly be illustrated in a lake ecosystem. In a lake ecosystem, the sun hits the water and helps the algae grow. Algae use carbon dioxide and water to make sugars and oxygen. The oxygen is useful for any eukaryote organism and the sugars provide food for the algae or anything that eats the algae, such as microscopic organisms. Small fish eat the microscopic animals, absorb oxygen with their gills and expel carbon dioxide, which plants then use to grow. If the algae disappeared, everything else would be impacted. Microscopic animals wouldn't have enough food, fish wouldn't have enough oxygen and plants would lose some of the carbon dioxide they need to grow.

Soil is also an important part of an ecosystem. It provides important nutrients for the plants in an ecosystem. It helps anchor the plants to keep them in place. Soil absorbs and holds water for plants and animals to use and provides a home for lots of living organisms. The atmosphere provides oxygen and carbon dioxide for the plants and animals in an ecosystem. The atmosphere is also part of the water cycle. Without the interactions among organisms and elements in the atmosphere, there would be no life at all.

[1] [2] [3]

Basic Functional Components

We can recognize four functional components of an ecosystem: 1) *abiotic factors*, 2) *producers*, 3) *consumers*, and 4) *decomposers*. The latter three are living components, what Odum (1959) termed the three "functional kingdoms of nature", so important and universal is their presence in ecosystems.

Abiotic Factors



An example of organisms that live in the intertidal zone

Abiotic factors can increase or decrease the amount of **environmental stress** on an ecosystem and therefore can also affect the stability of that ecosystem. We studied many of these in detail in (Chapter 4). Do not forget that physical (essentially geological) structure can influence ecological function: the nature of interactions of species in the sea can be very different from those in the atmosphere directly as a consequence of difference in physical properties of air and water.

The intertidal zone is the shore area that is submerged at high tide and exposed at low tide. It is rich in oxygen and nutrients and provides a home for many different species. The organisms that live in this area are constantly exposed to a **high stress**, **less stable** environment. However, they have adapted to huge daily changes in moisture, temperature, turbulence (from the water), and salinity. They have to be used to living in both wet and dry conditions continually. Water is a very powerful substance and the constant impact from the moving water can have drastic impacts on both living and non-living things. Intertidal organisms are forced to bury into the sand, hide under rocks and/or attach themselves to larger structures to avoid being carried away by the waves. Also, the constant flux of the environmental temperature is enough to make any creature uncomfortable. Since this area is exposed to both water and land, the organisms here must compete with predators that hunt at both areas.



A tropical forest on a polynesian island

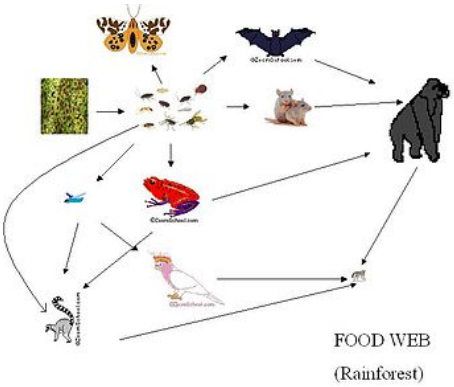
Jungles or rainforests are an example of a **low stress**, **more stable** environment that are vital to maintaining the ecosystems of the earth. Unlike the intertidal zone, this environment has more subtle changes that occur at a much slower rate. Jungles are very stable environments that possess some 40% of all species. It is also a very diverse environment consisting of several layers of organisms using different parts of the ecosystem. As well as increasing biodiversity, jungles are beneficial to increasing our knowledge of medicinal plants and increasing oxygen output. Since the rainforest is literally a smörgåsbord a plants and animals, discoveries are continually made of the beneficial nature of these organisms.

Read: Intertidal Zones

Food Webs

A **food web** is a series of interacting food chains. Food chains show the order in which animals consume food. Food chains and food webs are made up of Producers, Consumers, and Decomposers. **Producers** are Autotrophic Organisms. "Autotrophic" means self-nourishing. The most conspicuous group of autotrophs are the **photolithoautotrophs**, organisms such as algae and flowering plants that have cells containing chlorophyll and are thus capable of fixing light energy ("photo-") to build complex organic substances from simple inorganic substances ("litho-"). In the next chapter we are going to study the energetics of this process; now, we are mostly interested in how producers "create" organic matter utilizing energy and inorganic matter. The organic compounds that are created may be used structurally within the organism or may be latter broken down into inorganic matter and energy extracted by the process. **Consumers** are [Heterotrophic Organisms], which are also termed **macroconsumers**. A simple definition of a heterotrophic organism is a species that is dependent on organic matter for food. **Decomposers** are heterotrophic organisms. These are also termed microconsumers, saprobes, or saprophytes. Decomposers are scavengers that break down dead plants and animals.

Decomposers are vital to the food web because they break down and recycle nutrients back into the soil. These nutrients are then used by producers to sustain life. Without the enzymes that decomposers provide to breakdown organic material into inorganic material, phosphorous(P) and nitrogen(N), Producers would eventually die out and the main part of food webs would cease to exist and therefore life would cease to exist. Decomposers recycle material but they do not recycle energy. Solar irradiation still provides the energy that drives the life cycle.



A foodweb of rainforest organisms

Decomposition is a natural process but decomposers speed up the process of decomposition. Bacteria, fungi and actinomycetes are three main types of decomposers. Bacteria make up about 90% of all microorganisms and are the most abundant of decomposers. They can eat anything from dead trees, dead animals and oil slicks on the surface of the ocean. Fungi and actinomycetes work on harder substances like cellulose, bark, paper and stems. These decomposers usually only work to a certain stage in decomposition then bacteria will finish the process, similar to primary and secondary succession.

A study conducted in a California river by Mary Power showed the impact that fish had on the river food wed. The main fish studied in the experiment were the steelhead and roach, these fish at a juvenile stage consume insects and fish fry, which consume chironomid larvae. These larvae reduce the algae biomass in the river. She found that when the larger adult fish species were absent, smaller more abundant predators thrived and decrease the chironomid larvae population significantly, which allowed the algae biomass to increase. This results in more cyanobacteria and diatoms to flourish on the algal turfs[4]. This study showed a good example of how consumers and producers interact, and also showed that when one trophic level is disrupted it has a domino effect on the other trophic levels involved in the food web.

With Food Webs there are a few calculations that we can use to help us better understand the system. Chain Length is essentially the number of links between trophic levels. But when we calculate this we use the mean length. So to calculate Chain Length(CL) the equation is CL=(# of links/T-1) where T is equal to the number of trophic levels. We can also calculate link density(LD). LD=(# of Links/n) where n is the number of species in the web. And finally we can calculate Web Connectance(C). C=(actual links/potential links(N)) Where N=n(n-1)/2.

Food webs do pose some problems for ecological studies. Identifying trophic levels is very difficult in nature. Ecosystem boundaries are also tough to determine. Identifying all of the species in a community can be difficult. Quantifying and identifying the strengths of interactions is hard. In most cases it is very hard to determine what the eliminating nutrients are.

Biological Magnification

The focus of this chapter is trophic levels and nutrient transfer between trophic levels and the food webs. Not all transfers between trophic levels are positive. Biological Magnification is the tendency of pollutants to concentrate in successive trophic levels. The pollutants are usually toxic and cause death to the organism.

The first step in Biomagnification is when a producer takes up nutrients in the soil that it stores by accident as an essential nutrient. Producers will try to store massive amounts of nutrients, when "mistaken" nutrients are absorbed, i.e. DDT and Mercury, The concentration levels in the producers are greater than the levels in the surrounding environment. When the producer is eaten by the herbivore or omnivore the pollutants are transferred to the next trophic level. Since energy transfer between trophic levels is approximately ten percent, the next chain in the trophic level must try to consume large amounts of the previous trophic level to sustain life and the pollutant, once again, is concentrated in the next trophic level.

The pollutants, once absorbed, are stored in the bodies of the consumers. DDT and PCB's are fat soluble and when one trophic level is consumed by the other the fat moves from one consumer to the next. Water soluble pollutants usually cannot concentrate because they would easily dissolve in the organism. Polluted water leaves an organism rather easily whereas fat does not leave the body.

Three main criteria must be met for a pollutant to biomagnify:

1. The pollutant must be long lived.
2. The pollutant must be concentrated by the producers.
3. The pollutant must be fat-soluble.

Guild

Species competing for the same resources in similar fashion are known as guilds. They are classified according to how they acquire their nutrients, their state of mobility, and their mode of feeding. Some examples of guilds are forbs, geophytes, graminoids, shrubs, trees and vines. A guild is much more stable than a single species, since more than one species can balance out the system. In a study of feeding patterns on polychaetes, Fauchald and Jumars (1979) utilized feeding guilds as a method of generalization and determining phylogenetic relationships, indeed claiming that guilds were very useful in summarizing data into patterns [5].

In a 2009 study, a guild approach was used to evaluate the roles of foraging habitats and exposure timing, as well as tropic position on Mercury (Hg) bioaccumulation. Five species of waterbirds forming three distinct foraging guilds in the San Francisco Bay (SFB) estuary were used in this investigation. Because estuarine waterbirds form well-documented, distinct guilds distinguished by their feeding method and habitat use and because the SFB estuary has a legacy of Hg contamination from historic mining in the Sierra Nevada Coast Mountain Range, Hg exposure was able to be evaluated on both large-scale foraging strategies (such as tropic position) occurring among guilds and small-scale strategies (such as foraging micro-habitats) that occur within guilds. As indicated by this study, SFB waterbirds accumulated alarming Hg concentrations. Concentrations that place them at considerable risk to deleterious reproductive effects. Such exposure was shown to vary as a function of micro-habitat, region, trophic level, and time spent in the estuary. These results have raised quite a bit of concern because the SFB estuary is among the most important sites for wintering, migrating, and breeding waterbird populations along the Pacific Flyaway [6].



A bear is an example of a keystone species, which provides stability to a community.

Keystone Species

A keystone species is a species having a disproportionate effect on the ecosystem. They provide stability to an ecosystem. Normally they are not the dominant species but are required for a community to have stability. Many times, keystone species are predators that keep some type of herbivore from consuming all of the dominant plant species. One interesting aspect of keystone species is that, since they normally feed on predators that consume small numbers of prey, they can effectively control a system without actually needing to have a large population size.

J. Brown and E. Heske studied the effects of the removal of *Dipodomys* spp. (Kangaroo rats) from the Chihuahuan Desert shrub habitat in southeastern Arizona. Twelve years after the removal of three species of kangaroo rats, the controlled plots in the habitat went from shrubland to grassland. The density of perennial and annual grasses increased considerably, and other rodent species in the area colonized. These major changes in the ecosystem showed that the *Dipodomys* spp. have a significant effect on the diversity and biogeochemical processes, which led the researchers to believe that the kangaroo rats are a keystone species [7]. Some other examples of keystone species would include Starfish, Sea Otters, Bears, Beavers and Domestic Cats.

- Read: Keystone Species

All the examples of keystone species mentioned above are animals. However, this isn't always the case. *Pinus chiapensis* is an early successional, neotropical pine species found in warm, humid, mid-elevation Mesoamercian areas such as in the tropical montane areas of southern Mexico and western Guatemala. It has been discovered that forests dominated by *P. chiapensis* are the first to appear after disturbance, modifying drastically the environment by shading the forest floor, favoring soil development, increasing the rate of soil carbon sequestration, acidifying the soil, releasing nutrient cations by weathering the bed rock, and providing a source of food for birds and mammals. *P. chiapensis* trees inhibit their own development while facilitating the growth of broadleaved species typical of tropical montane cloud forests. Ultimately, *P. chiapensis*is a keystone species because of its crucial impacts in tropical montane cloud forest regeneration and its effect on ecosystem processes [8].

Hypotheses of Food Web Control

Each food web contains N numbers of trophic levels and with each number the cycle of dependence flip-flops according to the Oksanen's Model. There are two hypotheses involved in this model one is known as the **Bottom-up Control** hypothesis. The bottom-up control hypothesis states that both the top and the bottom trophic levels are controlled by resource limitations For example in a three tiered food web (three trophic levels), the bottom trophic level would contain a species of plants, which of course are dependent on the resources available to it. The next trophic level would be some species of herbivore, these herbivores are limited and controlled by a species of predator which is also the third trophic level. The predator or top trophic level is then limited by the plant resources keeping the herbivores alive and reproducing.

If we were to now add a trophic level, such as a secondary predator (the original predator being the primary predator), the cycle of dependence would then flip-flop, and the **Top-bottom Control** hypothesis would apply. The top-bottom control hypothesis states that the food web cycle is predator limited. We now have our plant species ==> the herbivore ==> the primary predator ==> and the secondary predator. The plants that were resource limited are now predator limited by the herbivores. The herbivores are now resource limited by the plants abundance. The primary predator is now limited by the secondary predator and the secondary predator is now limited by the resources of the primary predator, herbivore, and plants.

This cycle repeats itself and with each additional trophic level added, the limitation of the lower trophic levels changes from either resource limited or predator limited to the other. The relationships of two trophic levels when the bottom is resource limited and the top is predator limited gives a positive slope. The more of the lower trophic level the more there is of the upper trophic level. The inverse is true when the lower trophic level is predator limited and the upper trophic level is resource limited, it creates a negative slope the more are of the upper trophic level the less there will be of the lower trophic level.

For more detailed information on this trophic cascade idea and for examples read:Trophic cascade

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- Footnote:[1] Breathing is an activity at the organism level of biological complexity. The actual use of oxygen molecules and production of carbon dioxide molecules takes place at the cellular and subcellular levels. The exchange process within the vole involves tissue and organ level activities (lungs and circulatory system).

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7.3: ENERGY FLOW THROUGH ECOSYSTEMS

LEARNING OBJECTIVES

By the end of this section, you will be able to do the following:

- Describe how organisms acquire energy in a food web and in associated food chains
- Explain how the efficiency of energy transfers between trophic levels affects ecosystem structure and dynamics
- Discuss trophic levels and how ecological pyramids are used to model them

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.

It is important to understand how organisms acquire energy and how that energy is passed from one organism to another through food webs and their constituent food chains. 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.

HOW ORGANISMS ACQUIRE ENERGY IN A FOOD WEB

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. These ecosystems are often described by grazing food webs. 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 46.9). Many chemoautotrophs in hydrothermal vents use hydrogen sulfide (H_2S), 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.

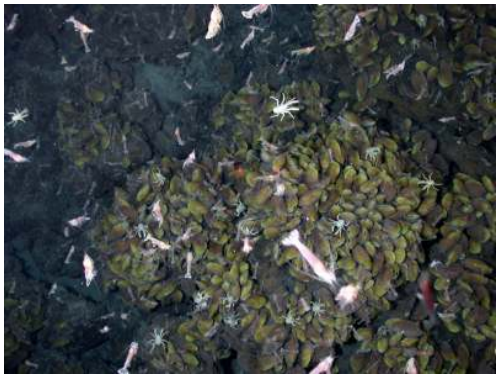


Figure 46.9 Swimming shrimp, a few squat lobsters, and hundreds of vent mussels are seen at a hydrothermal vent at the bottom of the ocean. As no sunlight penetrates to this depth, the ecosystem is supported by chemoautotrophic bacteria and organic material that sinks from the ocean's surface. This picture 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.

PRODUCTIVITY WITHIN TROPHIC LEVELS

Productivity within an ecosystem can be defined as the percentage of energy entering the ecosystem incorporated into biomass in a particular trophic level. Biomass is the total mass, in a unit area at the time of measurement, of living or previously living organisms within

a trophic level. Ecosystems have characteristic amounts of biomass at each trophic level. For example, in the English Channel ecosystem the primary producers account for a biomass of 4 g/m^2 (grams per square meter), while the primary consumers exhibit a biomass of 21 g/m^2.

The productivity of the primary producers is especially important in any ecosystem because these organisms bring energy to other living organisms by photoautotrophy or chemoautotrophy. The rate at which photosynthetic primary producers incorporate energy from the sun is called gross primary productivity. An example of gross primary productivity is shown in the compartment diagram of energy flow within the Silver Springs aquatic ecosystem as shown (Figure 46.8). In this ecosystem, the total energy accumulated by the primary producers (gross primary productivity) was shown to be 20,810 kcal/m^2/yr.

Because all organisms need to use some of this energy for their own functions (like respiration and resulting metabolic heat loss) scientists often refer to the net primary productivity of an ecosystem. Net primary productivity is the energy that remains in the primary producers after accounting for the organisms' respiration and heat loss. The net productivity is then available to the primary consumers at the next trophic level. In our Silver Springs example, 13,187 of the 20,810 kcal/m^2/yr were used for respiration or were lost as heat, leaving 7,633 kcal/m^2/yr of energy for use by the primary consumers.

ECOLOGICAL EFFICIENCY: THE TRANSFER OF ENERGY BETWEEN TROPHIC LEVELS

As illustrated in (Figure 46.8), as energy flows from primary producers through the various trophic levels, the ecosystem loses large amounts of energy. The main reason for this loss is the second law of thermodynamics, which states that whenever energy is converted from one form to another, there is a tendency toward disorder (entropy) in the system. In biologic systems, this energy takes the form of metabolic heat, which is lost when the organisms consume other organisms. In the Silver Springs ecosystem example (Figure 46.8), we see that the primary consumers produced 1103 kcal/m^2/yr from the 7618 kcal/m^2/yr of energy available to them from the primary producers. The measurement of energy transfer efficiency between two successive trophic levels is termed the trophic level transfer efficiency (TLTE) and is defined by the formula:

$$\text{TLTE} = \frac{\text{production at present trophic level}}{\text{production at previous trophic level}} \times 100$$

In Silver Springs, the TLTE between the first two trophic levels was approximately 14.48 percent. The low efficiency of energy transfer between trophic levels is usually the major factor that limits the length of food chains observed in a food web. The fact is, after four to six energy transfers, there is not enough energy left to support another trophic level. In the Lake Ontario example shown in (Figure 46.6), only three energy transfers occurred between the primary producer, (green algae), and the apex consumer (Chinook salmon).

Ecologists have many different methods of measuring energy transfers within ecosystems. Measurement difficulty depends on the complexity of the ecosystem and how much access scientists have to observe the ecosystem. In other words, some ecosystems are more difficult to study than others, and sometimes the quantification of energy transfers has to be estimated.

Other parameters are important in characterizing energy flow within an ecosystem. Net production efficiency (NPE) allows ecologists to quantify how efficiently organisms of a particular trophic level incorporate the energy they receive into biomass; it is calculated using the following formula:

$$\text{NPE} = \frac{\text{net consumer productivity}}{\text{assimilation}} \times 100$$

Net consumer productivity is the energy content available to the organisms of the next trophic level. Assimilation is the biomass (energy content generated per unit area) of the present trophic level after accounting for the energy lost due to incomplete ingestion of food, energy used for respiration, and energy lost as waste. Incomplete ingestion refers to the fact that some consumers eat only a part of their food. For example, when a lion kills an antelope, it will eat everything except the hide and bones. The lion is missing the energy-rich bone marrow inside the bone, so the lion does not make use of all the calories its prey could provide.

Thus, NPE measures how efficiently each trophic level uses and incorporates the energy from its food into biomass to fuel the next trophic level. In general, cold-blooded animals (ectotherms), such as invertebrates, fish, amphibians, and reptiles, use less of the energy they obtain for respiration and heat than warm-blooded animals (endotherms), such as birds and mammals. The extra heat generated in endotherms, although an advantage in terms of the activity of these organisms in colder environments, is a major disadvantage in terms of NPE. Therefore, many endotherms have to eat more often than ectotherms to get the energy they need for survival. In general, NPE for ectotherms is an order of magnitude (10x) higher than for endotherms. For example, the NPE for a caterpillar eating leaves has been measured at 18 percent, whereas the NPE for a squirrel eating acorns may be as low as 1.6 percent.

The inefficiency of energy use by warm-blooded animals has broad implications for the world's food supply. It is widely accepted that the meat industry uses large amounts of crops to feed livestock, and because the NPE is low, much of the energy from animal feed is lost. For example, it costs about $0.01 to produce 1000 dietary calories (kcal) of corn or soybeans, but approximately $0.19 to produce a similar number of calories growing cattle for beef consumption. The same energy content of milk from cattle is also costly, at approximately $0.16

per 1000 kcal. Much of this difference is due to the low NPE of cattle. Thus, there has been a growing movement worldwide to promote the consumption of nonmeat and nondairy foods so that less energy is wasted feeding animals for the meat industry.

MODELING ECOSYSTEMS ENERGY FLOW: ECOLOGICAL PYRAMIDS

The structure of ecosystems can be visualized with ecological pyramids, which were first described by the pioneering studies of Charles Elton in the 1920s. Ecological pyramids show the relative amounts of various parameters (such as number of organisms, energy, and biomass) across trophic levels.

Pyramids of numbers can be either upright or inverted, depending on the ecosystem. As shown in Figure 46.10, typical grassland during the summer has a base of many plants, and the numbers of organisms decrease at each trophic level. However, during the summer in a temperate forest, the base of the pyramid consists of few trees compared with the number of primary consumers, mostly insects. Because trees are large, they have great photosynthetic capability, and dominate other plants in this ecosystem to obtain sunlight. Even in smaller numbers, primary producers in forests are still capable of supporting other trophic levels.

Another way to visualize ecosystem structure is with pyramids of biomass. This pyramid measures the amount of energy converted into living tissue at the different trophic levels. Using the Silver Springs ecosystem example, this data exhibits an upright biomass pyramid (Figure 46.10), whereas the pyramid from the English Channel example is inverted. The plants (primary producers) of the Silver Springs ecosystem make up a large percentage of the biomass found there. However, the phytoplankton in the English Channel example make up less biomass than the primary consumers, the zooplankton. As with inverted pyramids of numbers, this inverted pyramid is not due to a lack of productivity from the primary producers, but results from the high turnover rate of the phytoplankton. The phytoplankton are consumed rapidly by the primary consumers, thus, minimizing their biomass at any particular point in time. However, phytoplankton reproduce quickly, thus they are able to support the rest of the ecosystem.

Pyramid ecosystem modeling can also be used to show energy flow through the trophic levels. Notice that these numbers are the same as those used in the energy flow compartment diagram in (Figure 46.8). Pyramids of energy are always upright, and an ecosystem without sufficient primary productivity cannot be supported. All types of ecological pyramids are useful for characterizing ecosystem structure. However, in the study of energy flow through the ecosystem, pyramids of energy are the most consistent and representative models of ecosystem structure (Figure 46.10).

VISUAL CONNECTION

VISUAL CONNECTION

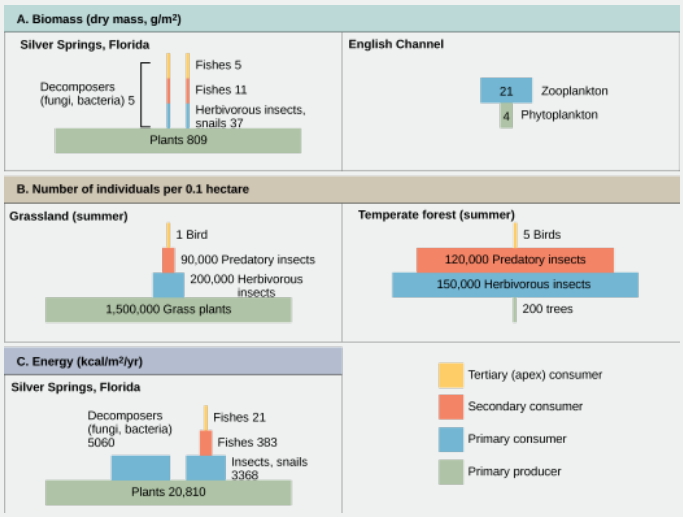


Figure 46.10 Ecological pyramids depict the (a) biomass, (b) number of organisms, and (c) energy in each trophic level.

Pyramids depicting the number of organisms or biomass may be inverted, upright, or even diamond-shaped. Energy pyramids, however, are always upright. Why?

CONSEQUENCES OF FOOD WEBS: BIOLOGICAL MAGNIFICATION

One of the most important environmental consequences of ecosystem dynamics is biomagnification. Biomagnification is the increasing concentration of persistent, toxic substances in organisms at each trophic level, from the primary producers to the apex consumers. Many substances have been shown to bioaccumulate, including the pesticide **d**ichloro**d**iphenyl**t**richloroethane (DDT), which was described in the 1960s bestseller, *Silent Spring*, by marine biologist Rachel Carson. DDT was a commonly used pesticide before its dangers became known.

In some aquatic ecosystems, organisms from each trophic level consumed many organisms of the lower level, which caused DDT to increase in birds (apex consumers) that ate fish. Thus, the birds accumulated sufficient amounts of DDT to cause fragility in their eggshells. This effect increased egg breakage during nesting and was shown to have adverse effects on these bird populations. Carson's combination of scientific knowledge and illuminating writing helped raise awareness about overall environmental issues as well as the specifics of the pesticide. The use of DDT was banned in the United States in the 1970s.

Other substances that biomagnify are polychlorinated biphenyls (PCBs), which were used in coolant liquids in the United States until their use was banned in 1979, and heavy metals, such as mercury, lead, and cadmium. These substances were best studied in aquatic ecosystems, where fish species at different trophic levels accumulate toxic substances brought through the ecosystem by the primary producers. As illustrated in a study performed by the National Oceanic and Atmospheric Administration (NOAA) in the Saginaw Bay of Lake Huron (Figure 46.11), PCB concentrations increased from the ecosystem's primary producers (phytoplankton) through the different trophic levels of fish species. The apex consumer (walleye) has more than four times the amount of PCBs compared to phytoplankton. Also, based on results from other studies, birds that eat these fish may have PCB levels at least one order of magnitude higher than those found in the lake fish.

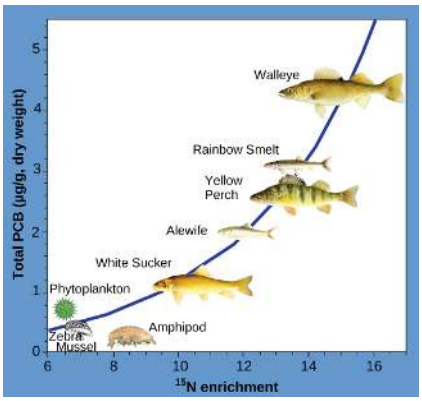


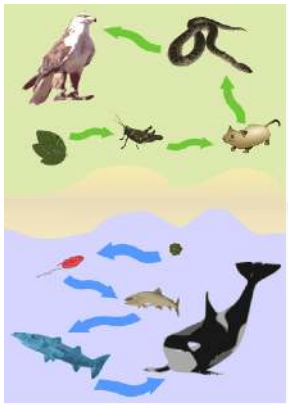
Figure 46.11 This chart shows the PCB concentrations found at the various trophic levels in the Saginaw Bay ecosystem of Lake Huron. Numbers on the x-axis reflect enrichment with heavy isotopes of nitrogen (^{15}N), which is a marker for increasing trophic level. Notice that the fish in the higher trophic levels accumulate more PCBs than those in lower trophic levels. (credit: Patricia Van Hoof, NOAA, GLERL)

Other concerns have been raised by the accumulation of heavy metals, such as mercury and cadmium, in certain types of seafood. The United States Environmental Protection Agency (EPA) recommends that pregnant people and young children should not consume any swordfish, shark, king mackerel, or tilefish because of their high mercury content. These individuals are advised to eat fish low in mercury: salmon, tilapia, shrimp, pollock, and catfish. Biomagnification is a good example of how ecosystem dynamics can affect our everyday lives, even influencing the food we eat.

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SECTION OVERVIEW

7.3.1: Energy in Ecosystems



An example of the concept of energy flow through trophic levels of a food chain.

There are several different factors that control the primary productivity of energy and biomass flow. Energy flow is the amount of energy that moves through a food chain. The energy input, or energy that enters the ecosystem, is measured in Joules or calories. Accordingly, the energy flow is also called calorific flow. In the study of energy flow, ecologists try to quantify the importance of different species and feeding relationships.

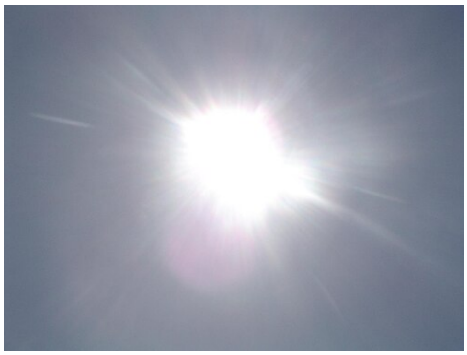
The largest source of energy for an ecosystem is the sun. Energy that is not used in an ecosystem is eventually lost as heat. Energy and nutrients are passed around through the food chain, when one organism eats another organism. Any energy remaining in a dead organism is consumed by decomposers. Nutrients can be cycled through an ecosystem but energy is simply lost over time.

An example of energy flow in an ecosystem would begin with the autotrophs that take energy from the sun. Herbivores then feed on the autotrophs and change the energy from the plant into energy that they can use. Carnivores subsequently feed on the herbivores and, finally, other carnivores prey on the carnivores.

In each case, energy is passed on from one trophic level to the next trophic level and each time some energy is lost as heat into the environment. This is due to the fact that each organism must use some energy that they received from other organisms in order to survive. The top consumer of a food chain will be the organism that receives the least amount of energy.

Hairston and Hairston (1993)^ , believe that there is a cause and effect relationship that results in any given trophic structure. Specifically, they state that it is trophic structure, rather than energetics that controls the amount of energy consumed at each trophic level and that "ecological efficiencies" are the product of a trophic structure, not a determining factor. Further, they state that trophic structure is instead the result of competition and predator-prey interactions. It is important to remember that many species may occupy each trophic level and are so subject to interspecific competition. This is especially true for producers, carnivores, and decomposers (Hairston, Smith, and Slobodkin, 1960)^ . Lastly it is not lost it is just consumed by its consumers.

Energy



The Sun is Most Common Source of Energy in Every Ecosystem

Energy is the ability to do work. Life manifests itself in energy changes, subject to the laws of thermodynamics. Ecosystems exist and operate by virtue of a flow of energy through the components of the system and thermodynamics (the movement of energy) forms the very basis of the biosphere organizing principles introduced in Chapter 2. Before proceeding into the relationship between ecology and thermodynamics, it is necessary to build a basic understanding of the physics of energetics, simply a further demonstration of the fact that ecology is multidisciplinary, requiring of its students a broad knowledge in all sciences.

- Read Energy - Follow links and cover details only as necessary to gain a basic understanding
- Read Laws of Thermodynamics - Read the expanded articles as needed to understand these basic principles of energy changes
- Read Principles of Energetics - You will find a constellation of related articles, including several with an ecological focus. You may wish to visit all of these to foster a deeper understanding

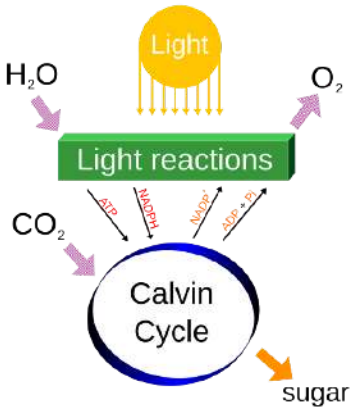
Although several sources of energy are available for exploitation on earth (e.g., geothermal, nuclear decay), the most significant is solar energy. Light and other radiation streaming out from the sun strikes the earth 93 million miles distant, providing energy to the atmosphere, the seas, and the land, warming objects that absorb this energy; that is, radiant energy is converted to heat energy (molecular motion). Differential heating causes winds and currents in the air and water, the heat energy becoming *kinetic energy* of motion. Warming results in evaporation of water into the atmosphere, setting up the hydrologic cycle (Chapter 4), the lifting of water into the atmosphere becoming *potential energy* that will convert to kinetic energy when the water begins to flow back downhill. However, the most significant solar energy driven process with respect to living systems is that of **photosynthesis**. Light energy is converted by photosynthesizing cells into a form of potential energy held in the chemical bonds of organic compounds. Organisms require both the substance and the stored energy of chemical compounds to function and grow, and eventually reproduce. Substance to provide the building blocks of cellular (and extracellular) components that comprise structure, and energy to move substances around, affect chemical reactions, and carry out all manner of intracellular and organismal processes.

Solar Constant

The **Solar Constant** is the average amount of radiant energy from the sun that reaches the Earth's atmosphere. This value is calculated at 2 calories per minute on each square centimeter of the Earth's upper atmosphere. This value can change because of Earth's elliptical path effecting seasonal changes and differences in the northern or southern slope which effect magnitude. The net radiation is what is left after some of the energy is reflected by the Earth's surface. Calculations for the solar constant are done by using the **astronomical unit (AU)** which is the mean distance between the Earth and Sun; One (AU) is equivalent to 92,960,000 miles (149,604,970 km).

Movement of the air and evaporation are important factors that regulate the temperature of the Earth from the sun's energy. The movements of air allow energy to be given off into space and without this reflection of energy the Earth would rapidly overheat and life would extinguish. This interaction is also a very important to the maintenance of the Earth's polar ice caps. A decrease in the solar constant of 2-5% would be enough to create a second ice age. Of course, as has been shown, the increasing use of industry by man, can increase earths temperature. If it were enough to cause the ice caps to melt, there would be an increase of approximately 7 degrees C. [1] This is due to the fact that the polar ice caps help in reflecting back the Earth's radiation. This reflection of the solar radiation is an essential part of the maintenance of the current climate that the Earth maintains. [2]

Organisms' Role in the Flow of Energy



A simplified overview of the process of photosynthesis.

When it comes to the flow of energy in ecosystems there are two types of organisms: **producers** and **consumers**. Plants are a common example of producers in all populations. They are able to convert carbon dioxide into oxygen and glucose, a common sugar consumed by most organisms. They do this through a process called photosynthesis which allows the plants to use sunlight as a source of energy. Producers convert energy from the environment into chemical energy in the form of carbon to carbon bonds. A classic example is the one previously mentioned where the plants convert CO_2 to O_2 and glucose.

The second type of organism is the consumer. Consumers are unable to make chemical energy the way plants do and have to use metabolic processes to get energy from carbon to carbon bonds, which is called respiration. Respiration breaks the carbon to carbon bonds and combines them with oxygen to make carbon dioxide. The energy released is used to help organisms move their muscles or as heat. Energy cannot be reused once it has been lost.

Read:

- Energy Flow Through the Ecosystem
- Ecosystems Background Information
- Ecology

Measuring Energy Flow

Flow diagrams are a visual way to understand how energy is transferred and/or transformed. A simple flow diagram usually starts with a primary producer[c]==> herbivore[c]==> predator[c]==> and so on. They can be as simple as that or as complex as the complete CO_2 cycle. The symbol [c] is the consumption rate of that species. The consumption rate between forcing functions is denoted by r, (r=[c]/t). The forcing function, which is the flow of energy between species, is usually measured in $kcalmol^{-1}year^{-1}$. The primary producer efficiency is measured by (NPP/Total consumed)x 100. Secondary production efficiency is measured by (NSP/Total consumed)x 100.

For more detailed examples visit: Energy Flow of Organisms

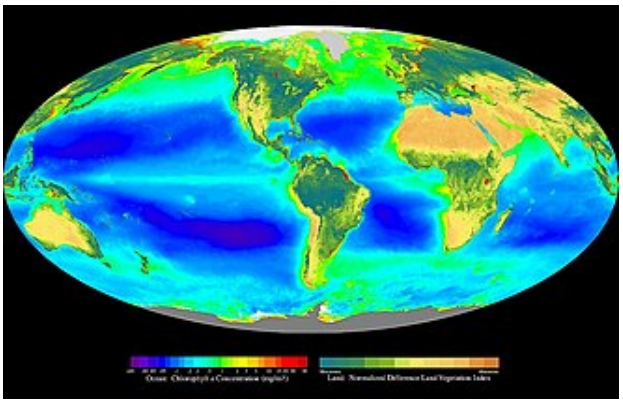
Primary and Secondary Production

The Net Primary Production(**NPP**) is the amount of carbon fixed per unit time (usually per day). Measures of net primary production include:

1. change in dry biomass per unit time
2. calorimetry
3. carbon dioxide uptake over time
4. oxygen uptake over time (comparison of the plant's light cycle to its dark cycle)
5. change in chlorophyll-a concentration, which equals the concentration of carbon dioxide fixed per day.

Ecologists look at dry mass because the high variability of water content makes accurate measurements difficult. Essentially about 95% of the dry mass is carbon and about 99.9% of the global biomass is plants (which includes algae, cyanobacteria, and other

organisms that contain chlorophyll).



Global oceanic and terrestrial photoautotroph abundance, from September 1997 to August 2000. As an estimate of autotroph biomass, it is only a rough indicator of primary production potential, and not an actual estimate of it.

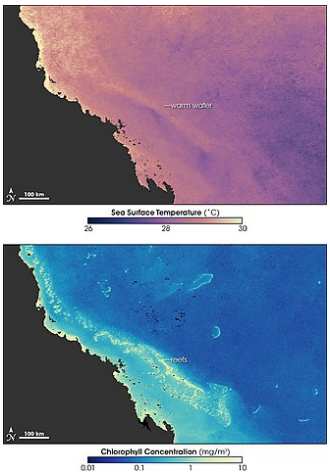
There are several different things that can limit NPP Terresterial limiting factors include:

1. water/precipitation,
2. sunligh/temperature, and
3. nutrients.

Aquatic limiting factors include:

1. sunlight/temperature, and
2. nutrients.

The NPP of aquatic ecosystems has been vastly affected by global warming. Global warming is the primary issue due to human impacts and gas emissions. Projected increases in carbon dioxide and temperature for the next 50 years exceed the amounts in which great coral reefs have flourished over the past half-million years. Coral reefs are at a serious decline due to temperature increases and coral bleaching. ..



Two images showing the relationship of water temperature to w:coral bleaching along the Great Barrier Reef. Warm pink and yellow tones show where sea surface temperatures were warm in the top image. The warmest waters are the shallow waters over the reef near the coast, where coral bleaching was most severe in the summer. The lower image shows chlorophyll concentrations, where high concentrations (yellow) generally point to a high concentration of phytoplankton in surface waters of the ocean. In this image, the bright yellow dots actually represent the coral reefs, and not surface phytoplankton.

An estimated 30% of coral reefs are severely damaged and about 60% of coral reefs may be lost by 2030. [3]Coral bleaching not only affects the coral reefs, but the diverse collection of species that interact with each other within the coral reef ecosystem. An example of this is the increased consuming of corallivorous fish on recently bleached coral (Pratchett et al. 2009).[4] Corallivorous fish were found to increase stress on recently bleached coral due to increased feeding. The increased feeding on already stressed

corals may have contributed to the mortality of bleached coral. The Corallivorous fish however, only increased consuming for the early stages of coral bleaching, and may be a good indication of coral mortality. Coral bleaching affects reefs at a regional and global scale, and has a huge impact on the NPP of coral reef ecosystems.

The net primary production is the main factor that limits the amount of net secondary production. Net secondary Production (**NSP**) determines the amount of biomass consumed and calculates the energy content of the consumed biomass. It also determines the amount of biomass and/or energy assimulated that is equivalent to an increase in the biomass of the consumer. In this case, a growth in biomass can be defined as a growth in individuals or growth in populations that includes reproduction. Most of the energy lost in secondary production comes from maintenance respiration. Secondary producers will consume oxygen and produce heat, which results in fairly inefficient production. Endotherms have a mean efficiency of about 2% and ectotherms have a mean efficiency of about 10%. There is a loss of energy due to respiration of 98% and 90%, respectively. All other organisms have a 30%-40% efficiency rate. All animals that live off plants(herbivores) are included in this group of secondary producers.

Limiting Nutrients



Excess Nitrogen can cause ill affects such as toxic algal bloom

As mentioned above nutrients can play a role in limiting the production of a community. Other than sunlight, primary productivity is limited by nutrient availability. A **limiting nutrient** is a nutrient which is found in the lowest relative concentrations such that an increase in this nutrient will increase primary productivity, while a decrease in this nutrient will decrease primary productivity. Typically, either phosphorus or nitrogen serves as a limiting nutrient within a given ecosystem, though water availability can also serve to limit the primary productivity of an ecosystem. Trace nutrients such as molybdenum and zinc are necessary for the growth of plants and can act as limiting agents even though they are in very small quantities. Aquatic communities can also have limiting nutrients that control how much production takes place. In freshwater ecosystems net primary production is limited by phosphorus, and in the ocean the limiting nutrient is iron.

Read: Limiting Nutrients

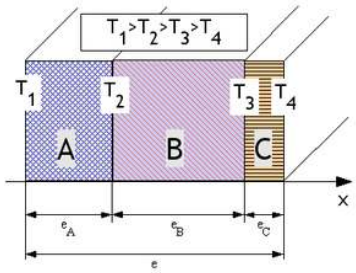
Too much of a nutrient can also have a limiting impact on a community. Recent studies have shown that excess nitrogen from human activities such as agriculture, energy production, and transport have begun to overwhelm the natural nitrogen cycle. The effects of the extra nutrients reach every environmental domain, threatening air and water quality and disrupting the health of terrestrial and aquatic ecosystems. In terrestrial ecosystems, nitrogen saturation can disrupt soil chemistry, leading to loss of other soil nutrients such as calcium, magnesium, and potassium. This means that while the nitrogen is not a limiting factor, it causes other nutrients in the soil to become limiting factors.

Read: Nutrient Overload

The Laws of Thermodynamics as they relate to Ecology

The laws of thermodynamics are fundamental concepts to chemical processes of the universe. They are extremely important in chemistry and physics, but are the basis for many biological concepts as well. The laws dictate how energy can be transported, which of course can be applied to ecology because energy transfer is what drives metabolism and, on a larger scale, food chains and food webs.

Zeroth Law of Thermodynamics



Since the temperature decreases going from block A to block C, assuming that all blocks are in thermal contact, heat energy will flow from the left to the right until all blocks are of equal temperature.

Zeroth Law of Thermodynamics is the most obvious of all three laws, simply stating that if the temperature of object A is equal to the temperature of object B, and the temperature of object C is equal to the temperature of object B then the temperature of object C equals the temperature of object A. Although this transitive property seems almost unnecessary to mention, it is of crucial importance to the subject of energy transfer in the form of heat energy, since temperature is a measure of heat. Its implications in ecology are obvious as well. Organisms require the means to survive in a climate of a certain range of temperatures, and evolution has created organisms with extremely different tolerances to temperature according to where they are located.

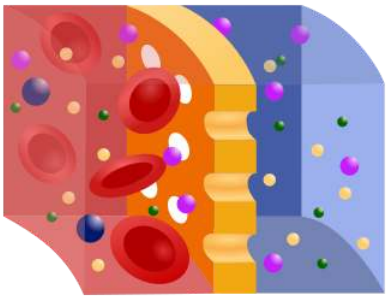
First Law of Thermodynamics

The **First Law of Thermodynamics** states that the total inflow of energy into a system must equal the total outflow of energy from the system, plus the change in the energy contained within the system. That is, energy is neither created nor destroyed, but may transform from one type to another. This is relevant to food webs in that the amount of energy being transferred through the food web cannot be larger than the amount of energy initially supplied by the primary producer (which was supplied by the sun's energy).

Second Law of Thermodynamics

The **Second Law of Thermodynamics** states that "energy of all kinds in our material world disperses or spreads out if it is not hindered from doing so." In other words, the randomness (entropy) of the universe is always increasing. This is quoted from a site devoted to demonstrating how the second law is involved in our open system of the earth and sun: http://www.entropysimple.com.

The second law of thermodynamics is definitely the most applicable of the four laws to ecology. It is consistent with Elton's Pyramid of foodwebs that states that although sometimes total size or number of organisms can either increase or decrease with increasing trophic levels, the total biomass ALWAYS decreases with increasing trophic levels, as energy is constantly being lost to the atmosphere (usually as CO_2. The energy from the sun allows living organisms on earth to temporarily decrease entropy, but our organized systems require an overall input of energy (provided by the sun). The second law of thermodynamics suggests a dire "heat death of the universe" will occur when all the energy of the universe is evenly distributed, and no life or concentrated matter (stars, galaxies) can exist, although this won't occur for at least 10^{100} years.



Semipermeable membranes are prevalent in many organisms and are a way that tendency toward entropy is manipulated to create a gradient. Such gradients can allow thermodynamically favorable reactions to occur yet maintain an organized structure.

Ecosystems are far from thermodynamic equilibrium, which used to be an argument against the second law of thermodynamics. Galucci (1973) [5] performed a literature review of the physical theory of thermodynamics in relation to mechanisms of energy

transfer in the environment (passive and active) and ecosystem productivity. He also studied how community structure and diversity related to entropy. As a result of his research, he claimed that the earth is a "receiver, reflector, and degrader of energy." The movement of energy through a community structure is necessary for its maintenance. External energy from the sun provides primary producers with energy and with a range of temperature in which life in the community is possible. Internal energy that travels from primary producers to organisms higher in the food chain is in the form of metabolism (mass, bonds) which provides transferrable energy. Galucci claimed that diversity is a form of entropy and improves the stability of a community. His conclusion was that the hypothesis of the second law of thermodynamics being applicable to ecosystems is supported.

Hedin *et al.* (1998) [6]studied biogeochemical processes involving nitrogen at soil to stream interfaces from a thermodynamic point of view. More than 1400 subsurface water samples from Michigan wetlands draining from a mixed forested-agricultural landscape were observed in this study. Thermodynamic principles could predict what form of nitrogen would be available to microbes if the number of electron donors and acceptors (water pH) is known. Microbes will transform nitrogen from NO_3^- to ammonia in acidic conditions present in shallow water, but covert NO_3 to N_2O gas in basic conditions present in deeper water. The findings agreed with this theory and were helpful because oxidizable carbon can be added to the shallow portions of the water that are not sufficient at denitrification. These findings would not have been possible (or understandable) if a thermodynamic approach to the metabolism of microorganisms had not been considered.

Third Law of Thermodynamics

The **Third Law of Thermodynamics** simply states that as temperature of a system reaches absolute zero (0 K), the entropy of the system decreases. Technically, it states that a system at absolute zero is at zero entropy, but this is theoretically not possible as it has been established that absolute zero is not able to be experimentally reached. This is why substances become gases (molecules spread out, entropy increased) at high temperatures, and freeze (become ordered crystalline structures, entropy decreased) at low temperatures. Decomposition also has a higher rate at higher temperatures for this reason.

Ecological Pyramids

An **Ecological Pyramid** (or **Trophic pyramid**) is a graphical representation designed to show the relationship between energy and trophic levels of a given ecosystem. Most commonly, this relationship is demonstrated through the number of individuals at a given trophic level, the amount of biomass at a given trophic level, or the amount of energy at a given trophic level. It is worth noting that all Ecological Pyramids begin with producers on the bottom and proceed through the various trophic levels, the highest of which is on top.

Pyramid of Biomass

An **Ecological Pyramid of Biomass** shows the relationship between energy and trophic level by quantifying the amount of biomass present at each trophic level (dry mass per trophic level). As such, is assumed that there is a direct relationship between biomass and energy. By doing this, the earlier discrepancy is avoided because even though there is only one tree, it is much more massive than the next trophic level.

The main problem with this type of Ecological Pyramid is that it can make a trophic level look like it contains more energy than it actually does. For example, all birds have a beak and skeleton, which despite taking up mass are not eaten by the next trophic level. In a **Pyramid of Biomass**, the skeleton and beak would still be quantified even though it does not contribute to the overall flow of energy into the next trophic level.

Pyramid of Energy (Ecology)

An **Ecological Pyramid of Energy** is the most useful of the three types, showing the direct relationship between energy and trophic level. It measures the number of calories per trophic level. As with the others, this graph begins with producers and ends with a higher trophic level.

When an ecosystem is healthy, this graph will always look like the standard **Ecological Pyramid** shown at the top of the page. This is because in order for the ecosystem to sustain itself, there must be more energy at lower trophic levels than there is at higher trophic levels. This allows for organisms on the lower levels to maintain a stable population, but to also feed the organisms on higher trophic levels, thus transferring energy up the pyramid.

When energy is transferred to the next trophic level, only 10% of it is used to build bodymass, becoming stored energy (the rest going to metabolic processes). As such, in a **Pyramid of Energy**, each step will be 10% the size of the previous step (100, 10, 1, 0.1, 0.01, 0.001 etc.).

The advantages of the Pyramid of Energy:

- It takes account of the rate of production over a period of time because each rectangle represents energy per unit area / volume per unit time. An example of units might be - kJ/m2/yr.
- Two species weight for weight may not have the same energy content therefore the biomass is misleading but energy is directly comparable.
- The relative energy flow within an ecosystem can be compared using pyramids of energy; also different ecosystems can be compared.
- There are no inverted pyramids.
- The input of solar energy can be added.

The disadvantages of the Pyramid of Energy:

- The energy value for a given mass of organism is required, which involves complete combustion of a sample.
- There is still the difficulty of assigning the organisms to a specific trophic level. As well as the organism in the food chains there is the problem of assigning the decomposers and detritivores to a particular trophic level.

The best way of showing what is happening in the feeding relationships of a community is to use Energy Pyramids.

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7.4: BIOGEOCHEMICAL CYCLES

LEARNING OBJECTIVES

By the end of this section, you will be able to do the following:

- Discuss the biogeochemical cycles of water, carbon, nitrogen, phosphorus, and sulfur
- Explain how human activities have impacted these cycles and the potential consequences for Earth

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. Geologic processes, such as weathering, erosion, water drainage, and the subduction 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.

Water contains hydrogen and oxygen, which is essential to all living processes. The hydrosphere is the area of the Earth where water movement and storage occurs. On or beneath the surface, water occurs in liquid or solid form in rivers, lakes, oceans, groundwater, polar ice caps, and glaciers. And it occurs as water vapor in the atmosphere. Carbon is found in all organic macromolecules and is an important constituent of fossil fuels. Nitrogen is a major component of our nucleic acids and proteins and 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 is critical to the 3-D folding of proteins, such as in disulfide binding.

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.

LINK TO LEARNING

LINK TO LEARNING

Head to this website to learn more about biogeochemical cycles.

THE WATER (HYDROLOGIC) CYCLE

Water is the basis of all living processes on Earth. When examining the stores of water on Earth, 97.5 percent of it is non-potable salt water (Figure 46.12). 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 that small amount of fresh surface water, a lack of which can have massive effects on ecosystem dynamics. To be successful, organisms must adapt to fluctuating water supplies. 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.

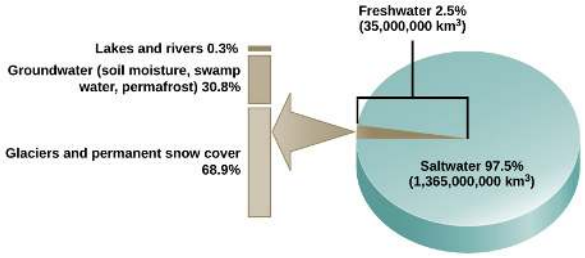


Figure 46.12 Only 2.5 percent of water on Earth is fresh water, and less than 1 percent of fresh water is easily accessible to living things.

Water cycling is extremely important to ecosystem dynamics. Water has a major influence on climate and, thus, on the environments of ecosystems. Most of the water on Earth is stored for long periods in the oceans, underground, and as ice. Figure 46.13 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.

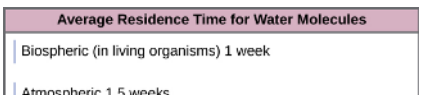


Figure 46.13 This graph shows the average residence time for water molecules in the Earth's water reservoirs.

There are various processes that occur during the cycling of water, shown in Figure 46.14. 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 permeates 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.

LINK TO LEARNING

LINK TO LEARNING

Head to this website to learn more about the world's fresh water supply.

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.

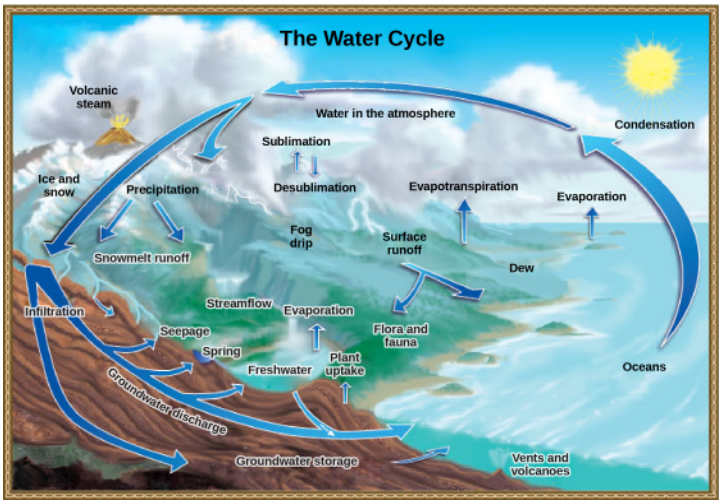


Figure 46.14 Water from the land and oceans enters the atmosphere by evaporation or sublimation, where it condenses into clouds and falls as rain or snow. Precipitated water may enter freshwater bodies or infiltrate the soil. The cycle is complete when surface or groundwater reenters the ocean. (credit: 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.

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 46.15.

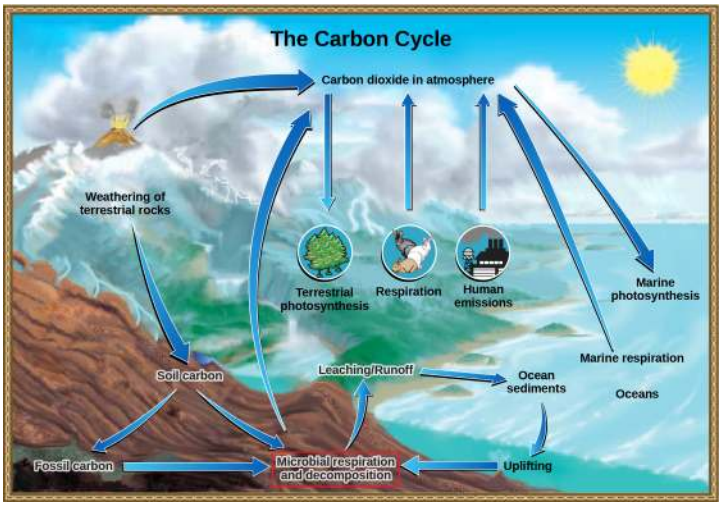


Figure 46.15 Carbon dioxide gas exists in the atmosphere and is dissolved in water. Photosynthesis converts carbon dioxide gas to organic carbon, and respiration cycles the organic carbon back into carbon dioxide gas. Long-term storage of organic carbon occurs when matter from living organisms is buried 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)

LINK TO LEARNING

LINK TO LEARNING

Click this link to read information about the United States Carbon Cycle Science Program.

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 multicarbon, 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 (Figure 46.16)

Step 1: CO_2 (atmospheric) ⇌ CO_2 (dissolved)
Step 2: CO_2 (dissolved) + H_2O ⇌ H_2CO_3 (carbonic acid)
Step 3: H_2CO_3 ⇌ + H^+ + HCO_3^- (bicarbonate ion)
Step 4: HCO_3^- ⇌ H^+ + CO_3^{2-} (carbonate ion)

Figure 46.16 Carbon dioxide reacts with water to form bicarbonate and carbonate ions.

The equilibrium coefficients are such that 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 nonrenewable resource because their use far exceeds their rate of formation. A nonrenewable 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.

Humans contribute to atmospheric carbon by the burning of fossil fuels and other materials. Since the Industrial Revolution, humans have significantly increased the release of carbon and carbon compounds, which has in turn affected the climate and overall environment.

Animal husbandry by humans also increases atmospheric carbon. 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 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.

THE NITROGEN CYCLE

Getting nitrogen into the living world is difficult. Plants and phytoplankton are not equipped to incorporate nitrogen from the atmosphere (which exists as tightly bonded, triple covalent N_2) 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. (For example, gardeners often grow peas both for their produce and to naturally add nitrogen to the soil. This practice goes back to ancient times, even if the science has only been recently understood.) 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 46.17, 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 reenter the atmosphere.

VISUAL CONNECTION

VISUAL CONNECTION

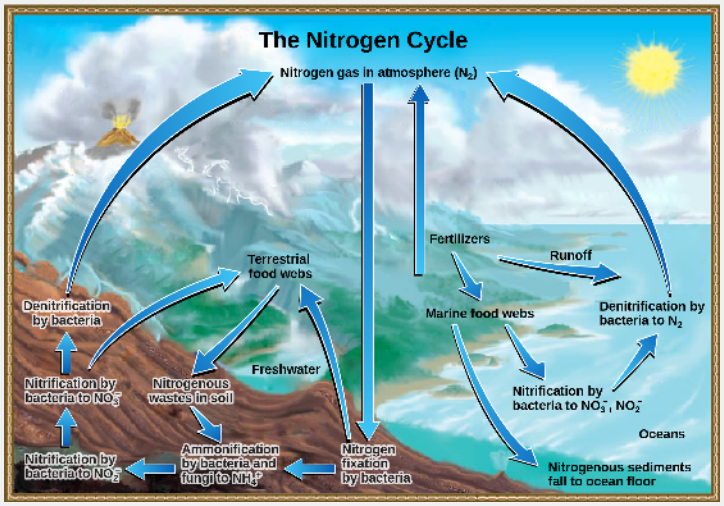


Figure 46.17 Nitrogen enters the living world from the atmosphere via nitrogen-fixing bacteria. This nitrogen and nitrogenous waste from animals is then processed back into gaseous nitrogen by soil bacteria, which also supply terrestrial food webs with the organic nitrogen they need. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

Which of the following statements about the nitrogen cycle is false?

1. Ammonification converts organic nitrogenous matter from living organisms into ammonium (NH_4^+).
2. Denitrification by bacteria converts nitrates (NO_3^-) to nitrogen gas (N_2).
3. Nitrification by bacteria converts nitrates (NO_3^-) to nitrites (NO_2^-).
4. Nitrogen fixing bacteria convert nitrogen gas (N_2) into organic compounds.

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.[3]

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 46.18).

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.

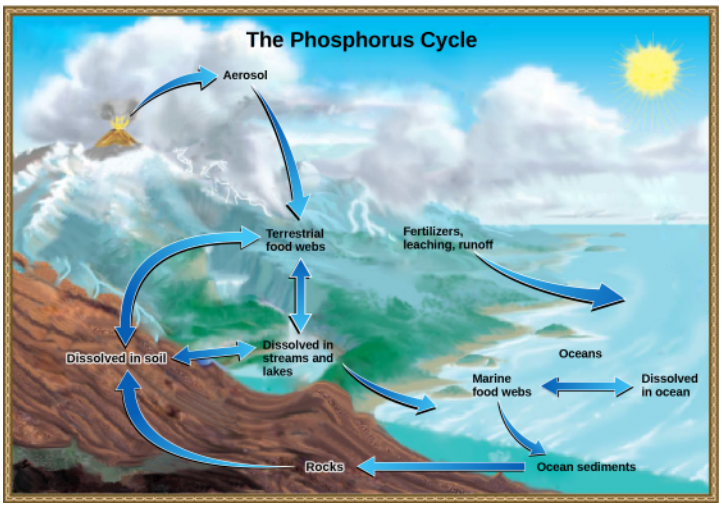


Figure 46.18 In nature, phosphorus exists as the phosphate ion (PO_4^{3-}). Weathering of rocks and volcanic activity releases phosphate into the soil, water, and air, where it becomes available to terrestrial food webs. Phosphate enters the oceans via surface runoff, groundwater flow, and river flow. 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)

As discussed in Chapter 44, 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 46.19).

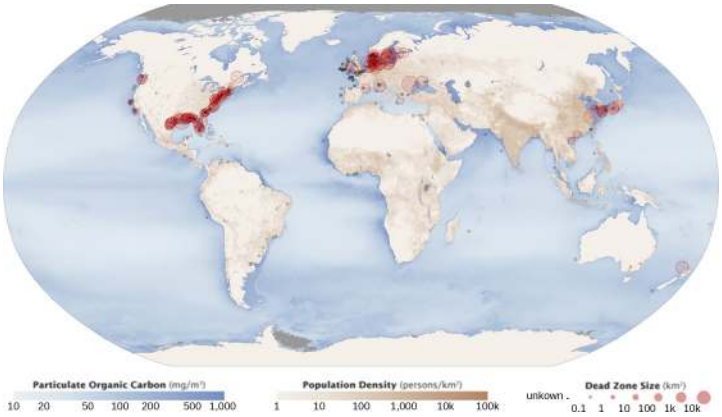


Figure 46.19 Dead zones occur when phosphorus and nitrogen from fertilizers cause excessive growth of microorganisms, which depletes oxygen and kills fauna. Worldwide, large dead zones are found in coastal areas of high population density. (credit: NASA Earth Observatory)

As discussed earlier, 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.

EVERYDAY CONNECTION

EVERYDAY CONNECTION

Chesapeake Bay



Figure 46.20 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 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. 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 nonprofit 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 interstate 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.

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 46.21, 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.

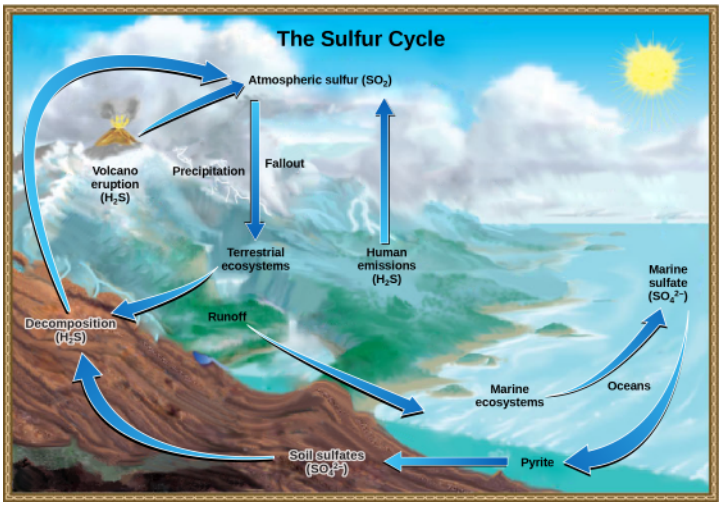


Figure 46.21 Sulfur dioxide from the atmosphere becomes available to terrestrial and marine ecosystems when it is dissolved in precipitation as weak sulfurous acid or when it falls directly to the Earth as fallout. Weathering of rocks also makes sulfates available to terrestrial ecosystems. Decomposition 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 46.21). 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 sulfurous acid (H_2SO_3). 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^-), and upon the death and decomposition of these organisms, release the sulfur back into the atmosphere as hydrogen sulfide (H_2S) gas.



Figure 46.22 At this sulfur vent in Lassen Volcanic National Park in northeastern California, the yellowish sulfur deposits are visible near the mouth of the vent.

Sulfur enters the ocean via runoff from land, from atmospheric fallout, and from underwater geothermal vents. Some ecosystems (Figure 46.9) rely on chemoautotrophs using sulfur as a biological energy source. This sulfur then supports marine ecosystems in the form of sulfates.

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 from coal, releases larger amounts of hydrogen sulfide gas into the atmosphere. Acid rain is caused by rainwater falling to the ground through this sulfur dioxide gas, turning it into weak sulfuric acid. 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.

LINK TO LEARNING

LINK TO LEARNING

Click this link to learn more about global climate change.

FOOTNOTES

- 3Scott 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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SECTION OVERVIEW

7.4.1: Biogeochemical Cycles



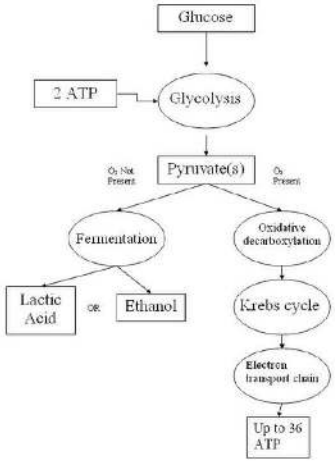
Planet earth from space

In the previous chapter on environmental response, we considered the various ways that individual organisms respond to the physical, chemical and/or biological stimuli in their environment.In this chapter, we will go deeper into the interactions between the biotic and the abiotic elements of the biosphere, focusing on the nonliving components. To begin to understand this concept: the physical "home" of our **biosphere**, we first have to consider the physics of planet formation. From all we know about life in the universe, only planets can possibly offer conditions suitable for life. And indeed, since all life we know of occurs on just one planet, we need to develop an understanding of what is special or unique about our home planet. How is the earth constituted; what is the nature of this "stage" upon which life developed and upon which life continues to play out. Presently, the "ecology" of other planets, if such a thing exists, is a subject of study within the science of **exobiology**.

Nutrients move through the ecosystem in biogeochemical cycles. A biogeochemical cycle is a circuit/pathway by which a chemical element moves through the biotic and the abiotic factors of an ecosystem. It is inclusive of the biotic factors, or living organisms, rocks, air, water, and chemicals. The elements that are moving through the biotic or abiotic factors may be recycled, or they may be accumulated in a place called a **sink/reservoir** where they are held for a long period of time. The amount of time that a chemical is held in one place is called **residence**.

All the chemical elements in an organism are part of the biogeochemical cycle. The chemicals travel not only through the biotic and abiotic components of an ecosystem, but they also travel through an organism. The abiotic factors of an ecosystem include: (1) water (hydrosphere), (2) land (lithosphere), and (3) air (atmosphere). All of the living factors that are found on Earth make up the biosphere.

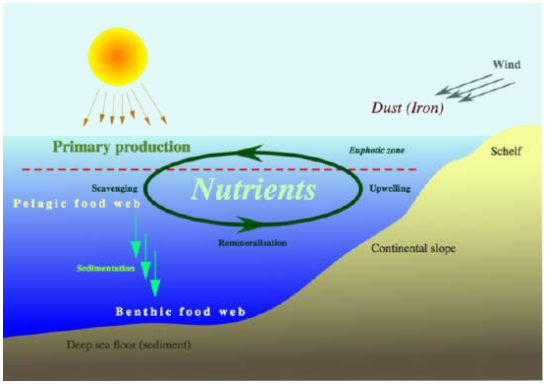
Nutrient Cycle Levels



Respiration can be both aerobic (in the presence of oxygen) and anaerobic (with out oxygen).

Nutrient cycles are broken up into three levels. There are **global nutrient cycles**, which occur when ecosystems become linked on a global scale. This is now known as an *Ecosphere*. On a smaller scale, there are **local nutrient cycles**. These cycles consist of the cycling that occurs in just one ecosystem. The smallest level includes **common nutrient budgets and fluxes**; some examples of this are carbon, H_2O, nitrogen, phosphorus, iron, and other trace elements. All of these cycles can be linked so that a community can remain at equilibrium. All of these cycles are driven by microbes. Microbes contain 350-550 giga tons of the worlds carbon. They also contain 85-130 giga tons of nitrogen, along with 9-14 giga tons of phosphorus. Nitrogen is only fixed by bacteria and archea, and they fix 85% of the 15 giga tons of nitrogen every year. Cyanobacteria are responsible for fixing 50% of the O_2 in the Ecosphere. There are also huge reserves of carbon locked up in rocks. Rocks contain 81 million gig tons of carbon, which is in the form of calcium carbonate ($CaCo_3$), commonly called limestone.

The processes that make up these cycles can be divided into two groups. The first group of processes all have an **aerobic component**. Through respiration, organic material can be converted into carbon dioxide. Respiration is done by animals, plants, and microbes. A second aerobic process is carbon fixation. This is the reverse of respiration where carbon dioxide is converted into organic material. The second group of processes are **anaerobic processes**. The first anaerobic process is fermentation. This is another way that organic material can be converted into carbon dioxide. Bacteria and fungi carry out this process when deprived of oxygen. A second form of an anaerobic process is carbon fixation. The only organisms that fix carbon anaerobically are archea. The last anaerobic process is methanogenesis. This process takes carbon dioxide and converts it into methane. This process is also only done by archea, but does not account for all methane because some methane can be made aerobically.



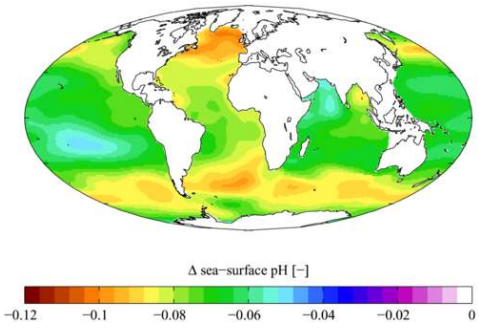
The Nutrient Cycle

There are two main types of systems on Earth, a closed system and an open system. A **closed system** occurs when the chemicals or elements used in an ecosystem are recycled instead of being lost. An **open system** occurs when the sun provides Earth with energy in the form of light which is usually used and then lost in the form of heat as it travels through the various trophic levels on Earth.

Although the biogeochemical cycles are complex and differ between the needs of nutrients by heterotrophs and autotrophs, there are three shared components of nutrient cycles: inputs, internal cycling, and outputs. Precipitation is one form of input, which brings appreciable quantities of nutrients into a cycle (Patterson, 1975). Microbes recycling dead organic material back into the system to be reused is a form of internal cycling. The export of nutrients must be offset by the input of nutrients into a system if there is to be no net loss. Carbon is exported from a cycle in the form of CO_2 via respiration of all living organisms.

The most important biogeochemical cycles are the carbon cycle, nitrogen cycle, oxygen cycle, phosphorus cycle, and the water cycle. The biogeochemical cycles always have a state of equilibrium. The state of equilibrium occurs when there is a balance in the cycling of the elements between compartments. Ecologists may also be interested in the sulfur cycle, the nutrient cycle, and the hydrogen cycle; however, ecologists are more interested in studying the carbon, nitrogen, oxygen, phosphorus, and water cycles.

The term biogeochemical gets its name from the previous cycles listed above (abiotiv factors). The prefix *Bio* refers to the biosphere. *Geo* refers to the lithosphere, atmosphere, and hydrosphere. Chemical refers to the various chemicals that go through/travel through the biogeochemical cycles.



global changes in earth's hydrosphere

A **biogeochemical cycle** or inorganic-organic cycle is a circulating or repeatable pathway by which either a chemical element or a molecule moves through both biotic ("bio-") and abiotic ("geo-") compartments of an ecosystem. In effect, an element is chemically recycled, although in some cycles there may be places (called "sinks") where the element accumulates and is held for a long period of time. In considering a specific biogeochemical cycle, we focus on a particular element and how that element participates in chemical reactions, moving between various molecular configurations. Of the 90-odd elements known to occur in nature, some 30 or 40 are thought to be required by living organisms (Odum, 1959). We will be considering only a few of these, mainly those utilized in fairly large quantities by living organisms. The principal elements of life are **carbon**, **hydrogen**, **oxygen**, and **nitrogen**. However, a number of others are certainly important to understand as well, notably **phosphorus** and **sulfur**. Some "non-essential" elements participate in biogeochemical cycles, entering organism tissues because of chemical similarity to essential elements. For example, strontium can behave like calcium in the body.

Hydrologic Cycle (Water Cycle)

A very significant molecule (on planet Earth) that cycles through ecosystems is the water molecule (H_2O). One of the reasons that life is so dependent on water is that it is the medium of chemical reactions within cells. While it generally is the case that we discuss the water cycle in terms of the various states of water, at least some water molecules are taken up by plants and split apart (photolysed) into atoms of hydrogen and oxygen; the latter is released into the atmosphere as molecular oxygen (O_2). Thus, by virtue of photosynthesizing organisms (*photoautotrophs*), the water cycle is an important part of both the oxygen and the hydrogen cycles. Note that hydrogen ends up as part of an organic molecule, and therefore a participant in the carbon cycle.

The majority of water in the water cycle is found within the oceans and the polar ice caps, although water is present in the bodies of organisms, in freshwater lakes and rivers, frozen in glaciers, and in the ground as groundwater. Water moves more or less freely between these storage reservoirs: by evaporation, by precipitation, and by runoff from the land.

The sedimentation cycle is an extension of the hydrological cycle. The water carries materials from the land to the ocean, where they are added as sediments. The sediment cycle includes the physical and chemical erosion, nutrient transport, and sediment formation from water flows. The sediment formed from water flows is mostly responsible for the buildup of sediments at the bottom of the ocean. The sediment cycle is tied in with the flow of six important elements, which are hydrogen, carbon, oxygen, nitrogen, phosphorus and sulfur. These elements, also known as macroelements, make up 95% of all living things. The balancing of these molecules is required to sustain life. These elements have to be recycled for life to continuously regenerate.



Carbon is being released into the atmosphere.

Carbon is required for the building of all organic compounds. Carbon in the form of carbon dioxide (CO_2) is obtained from the atmosphere and transformed into a usable organic form by organisms. The reservoirs for the carbon cycle are the atmosphere, where carbon dioxide exists as a free gas, fossil organic deposits (such as oil and coal), and durable organic materials like cellulose. Mineral carbonates, such as limestone, are a significant geological sink for carbon. During the process of carbon fixation, carbon dioxide is taken up from the atmospheric reservoir (or from biocarbonates dissolved in water) by plants, photosynthetic bacteria, and algae and is "fixed" into organic substances. Animals obtain their requirements for carbon (as carbon-based molecules) by eating plants or other animals. For the biological links, the carbon cycle comes full cycle when carbon is released by either plants and animals as they respire or after life as they decompose. Organisms respire carbon dioxide as a waste product from the breakdown of organic molecules as their cells derive energy from oxidizing the molecules containing "fixed" carbon. The burning of organic material such as wood or fuels also results in the release of carbon dioxide from organic carbon.

CO_2 is a trace gas and has huge effects on Earth's heat balance by absorbing infrared radiation. During the growing season or summer, there is a decrease in atmospheric CO_2 because increased sunlight and temperature helps plants increase their carbon dioxide uptake and growth. In the winter time, more CO_2 enters the atmosphere than can be removed by plants. This happens because plant respirations and the death of plants happens faster than photosynthesis. [Life and Biogeochemical Cycles]

Carbon Cycling Experiments

The impact of land-cover and land-use change on global carbon cycle has been the focus of various studies. The Brazilian Legal Amazon has been an area of particular interest because of rapid forest clearing. In determining such an impact, models are often developed and used. In a study focusing on the net carbon flux caused by deforestation and forest re-growth over the period of 1970-1998, a processed-based model of forest growth, carbon cycling, and land-cover dynamics was developed. This model was named CARLUC (for CARbon and Land-Use Change). This model, in particular, was used to estimate the size of terrestrial carbon pools in terra firme (unflooded) across the Brazilian Legal Amazon and the net flux of carbon resulting from forest disturbance and forest recovery from disturbance [1].

As previously mentioned, carbon cycling is driven by both abiotic and biotic factors. Net carbon fluxes can be partitioned into assimilatory and respiratory components. The complex interplay between assimilatory and respiratory sources and their responsiveness to abiotic changes such as drought and temperature are poorly understood. In a recent study, net carbon partitioning was used to disentangle abiotic and biotic drivers of all component influencing the overall sink strength of a Mediterranean ecosystem during a rapid spring to summer transition (between May and June 2006). It was ultimately determined that decreasing soil water availability rather than increasing air temperature largely affected both assimilation and respiration fluxes of understory plants and in consequence ecosystem respiration and soil respiration [2].

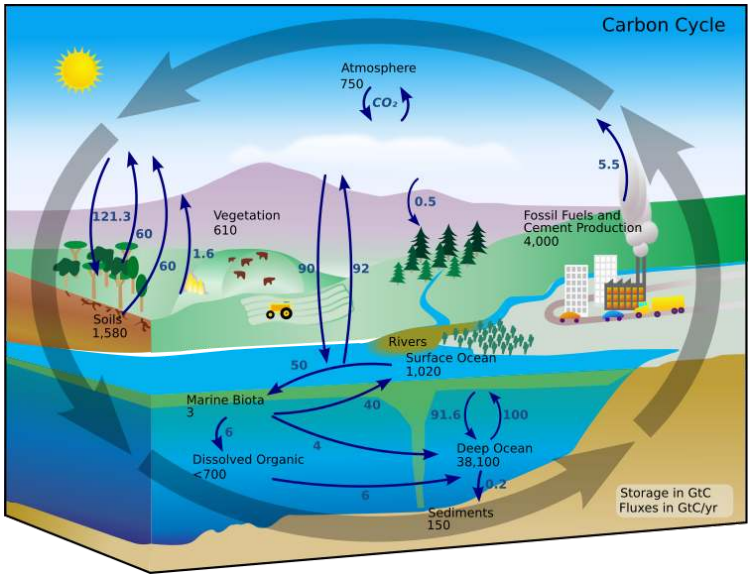
Global Carbon Cycle

Carbon is continuously cycled between the oceans, land, and the atmosphere. The atmospheric carbon is primarily carbon dioxide. Carbon on land occurs primarily in living biota and decaying organic matter. Dissolved carbon dioxide and small organisms like plankton that store carbon dioxide are major sources in the ocean. Carbon is measured in Gigatons, with the deep ocean containing almost 40,000 Gt, compared to about 2,000 Gt on land and 750 Gt in the atmosphere.

Carbon dioxide, a known "greenhouse gas," traps some of the radiation in the atmosphere that would be lost into space. This causes the atmosphere to be warmer than it would naturally be. Since pre-industrial times, man-made emissions have increased the amount

of carbon dioxide in the atmosphere by about 30%. The increase in carbon dioxide causing global warming is important for us to understand so we can predict future implications concerning our planet.

Average global temperatures have increased this past century and are predicted to increase even more in the next century. In a study done by Parmesan *et al*, the distribution and population dynamics of several species of butterflies were monitored in response to the increased temperatures. Migratory patterns of each species were observed and compared to previous patterns of distribution. The butterflies showed a northern shift, which is thought to be a response to increased temperatures. Parmesan *et al* concluded that the current and future climate warming may be a big factor in shifting species distributions [3].



Global Carbon Cycle

Nitrogen Cycle

Nitrogen is required for the manufacturing of all amino acids and nucleic acids; however, the average organism cannot use atmospheric nitrogen for these tasks and, as a result, is dependent on the nitrogen cycle to source usable nitrogen. The nitrogen cycle "begins" with nitrogen stored in the atmosphere as N_2 (the largest nitrogen reservoir). Nitrogen is also stored in the soil as ammonium (NH_4^+), ammonia (NH_3), nitrite (NO_2^-), and nitrate (NO_3^-). Nitrogen is assimilated into living organisms through three stages: nitrogen fixation, nitrification, and plant metabolism. Nitrogen fixation is a process that occurs in prokaryotes in which N_2 is converted to NH_4^+. Atmospheric nitrogen can also undergo nitrogen fixation by lighting and UV radiation and become NO_3^-. Following nitrogen fixation, nitrification occurs. During nitrification, ammonia is converted into nitrite, and nitrite is converted into nitrate. Nitrification occurs in various bacteria. In the final stage, plants absorb ammonia and nitrate and incorporate it into their metabolic pathways. Once the nitrogen has entered the plant metabolic pathway, it may be transferred to animals when the plant is eaten. Nitrogen is released back into the cycle when denitrifying bacteria convert NO_3^- into N_2 in the process of denitrification, when detrivorous bacteria convert organic compounds back into ammonia in the process of ammonification, or when animals excrete ammonia, urea, or uric acid.

A lot of environmental problems are caused by the disruption of the nitrogen cycle by human activity. Some of the problems caused range from the production of tropospheric (lower atmospheric) smog to the perturbation of stratospheric ozone and contamination of ground water. An example of one of the problems caused is the formation of greenhouse gas. Like carbon dioxide and water vapor, nitrous oxide traps heat near the earth's surface, and it also destroys the stratospheric ozone. Nitrous oxide in the earth's atmosphere is broken down by UV light into nitrogen dioxide and nitric oxide. These two products can reduce the ozone. Nitrogen oxides can be changed back into nitrates and nitrite compounds and recycled back into the earth's surface.[Environmental Biology - Ecosystems]

Phosphorus, Iron, and Trace Mineral cycles

The phosphorus cycle is one of the slowest biogeochemical cycles. Phosphorus mainly cycles through water, soil, and sediments. The little phosphorus in the atmosphere is carried by dust particles and such. Phosphate is most often in the form of phosphate

salts, which are released from weathered rock and dissolved in ground water where plants take them up. Phosphorus is a limiting factor for plants on land and in water, including the ocean, because there is so little of it, and it is not very soluble in water. The cycle does speed up a little bit as it cycles through plants and animals. When the plants and animals die and decay, the phosphorus is returned to the soil and sediments and eventually locked back in the rock.

The iron cycle is similar to every other cycle. Iron is, however, much more abundant than phosphorus. One additional way iron gets cycled, besides rock weathering, is when a volcano erupts and sends an iron-rich dust into the atmosphere, where it eventually spreads to soil and water.

Other trace minerals, such as zinc, copper, and manganese, were once thought to be just as abundant as nitrogen, carbon, and oxygen. Their depletion is thought to be from water erosion of the soil and over cropping of land, so that they aren't able to replenish themselves quickly enough. To learn more about all the trace minerals essential to life visit: Nutrients - Trace Minerals

"Perfect" Cycles

Odum (1959) describes what are called more or less "perfect" cycles: biogeochemical cycles that involve equilibrium states. That is, there exists in nature a balance in the cycling of the element between various compartments, with the element or material moving into abiotic compartments about as fast as it moves into biotic compartments. Certain ecosystems may experience "shortages," but overall, a balance exists on a global scale.

II. Deserts are characterized by their limited precipitation. Deserts have a brief rainy season, which on average produces less than 30 cm rainfall per year. Deserts are mainly located at 30 degrees North and South latitude because of their dry air resulting from the Hadley cells (please read interlink below on a Hadley cell), which stretch between the equator and 20 to 35 degrees North and South latitude.

Deserts have the capacity to be very productive climates because they are in a high energy input area of the round earth (please refer to chapter 3 about solar irradiation and the earth being round), but they are limited by their low precipitation. Desert flora or plant life is located on only 10% of desert area. They consist of mainly annuals that grow and reproduce during the brief rainy season. The main flora are succulents that store water, have waxy cuticles to prevent water loss, may have few modified small leaves or needles, and have large, shallow root systems.

III. Chaparrals are desert types located in the Mediterranean area. Chaparrals are characterized by their distinct rainy seasons and more so by their extremes. Summer temperatures can reach a high of approximately 40 degrees Celsius, and winter temperatures can reach a low of approximately -15 degrees Celsius. Plant and animal inhabitants are drought adapted to aide survival. Plant life is similar in characteristics to desert plants, with mainly shrub/brush type species.

Soil

Soil is the foundation for terrestrial systems. It is a mixture of organic (living and nonliving) and inorganic material. The organic part is contributed by plants, animals, and microbes. The inorganic part is a result of weathering.

Soil Layering

Soil is a composition of many different layers. The first(top) layer is the **O Horizon** which is then compsed of 2 sublayers the O_i and O_a layers. The O_i is the intact organic layer which is made up of dead organic matter and leaf litter. The O_a is contains mostly humus and is situated next to the A Horizon. The entire O Horizon is about 10cm deep. Deserts usually lack the O Horizon.

The next layer is the **A Horizon**. This is what most consider the topsoil, it is a mixture of weathered rock(clay, sand, and silt) from lower layers and organic material from the O Horizon. This is the area where there are the most roots, microbes, and invertebrates. This horizon usually has a high respiration rate, and has most of the nutrients leeched to lower layers by water. The top 2 layers combined (O and A Horizons) are on average about 0.5m deep.

The next layer is the **E Horizon** (or Eluviation Horizon). This layer has the least amount of dissolved nutrients. This layer can have a clay pan formed at the bottom which is highly compacted clay which prevents weathering of rock below. The also prevents tap roots from reaching the C Horizon. This may also cause the area above to become water-logged.

Below the E horizon is the Illuviation Horizon of **B Horizon**. This is the area where leechates collect, and most tap roots exist. It is usually mineral rich and contains little organic material. It is usually about 0.5m deep. Below the B Horizon is the **C Horizon**,

which is the lowest soil, layer is commonly called the subsoil. This is mostly weathered parent material. This is usually about 0.5m deep also.

Lastly is the inorganic material of the soil or the **R Horizon**. This is also called bedrock which is a result of weathering from wind, water, temperature, and plants.

Particle Size



Different sizes of particles in sand

The particle size of soil is correlated to the amount of surface area of the particles and the charge of the surface area. A decrease in particle size equals an increase in surface area which in turn equals an increase in a negative charge of the surface area. The United States Department of Agriculture (USDA) designates types of soil by the size of the particles in the soil. Clay consists of particles smaller than 0.002mm and has the largest water capacity and highest nutrient capacity. Silt consists of particles smaller than 0.05mm and has a relatively median water capacity and a median nutrient capacity. Sand consists of particles smaller than 2mm and has the smallest water capacity and the lowest nutrient capacity.

Acidic Soil

Acidic soil is any type of soil that has a low pH. It is created whenever soil is very low in minerals and may be created by conifer needles. Amino acids also breaks down clay. The breakdown of clay is done by leeching the minerals out of the soil. This leeching of minerals is due to a high Hydronium ion [H+] concentration which results of in less productive soil. Acid rain or precipitation that is unusually acidic because of emissions of sulfur and nitrogen compounds which react with the atmosphere is widely believed to be responsible for acidifying soil.

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7.5: 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 of the soil, but also climate, topography, and organisms living in the soil. In agriculture, the history of the soil, such as the cultivating practices and previous crops, modify the characteristics and fertility of that soil.

Importance of Soil

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. Through their roots, plants absorb water and minerals (e.g., nitrates, phosphates, potassium, copper, zinc). With these and carbon dioxide acquired during photosynthesis, plants produce carbohydrates, proteins, lipids, nucleic acids, and the vitamins, on which consumers depend.

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.

Several elements are considered essential for plant growth. Carbon (C), hydrogen (H), and oxygen (O) are required in large quantities, but they are not absorbed as mineral nutrients from the soil. Plants obtain carbon from carbon dioxide in the atmosphere and hydrogen from the water absorbed by the roots. Oxygen atoms come from carbon dioxide acquired during and gaseous oxygen in the atmosphere (acquire through aerobic cellular respiration) as well as water. 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.

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 **7.5.*a***).



Figure **7.5.*a***: These native plants are affected by herbicides that were used to kill nearby weeds. Image by Matt Lavin (CC-BY-SA).

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. However, some nutrients are selectively absorbed by the root membranes, enabling concentrations to become higher inside the plant than in the soil.

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 (figure **7.5.*b***). 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.

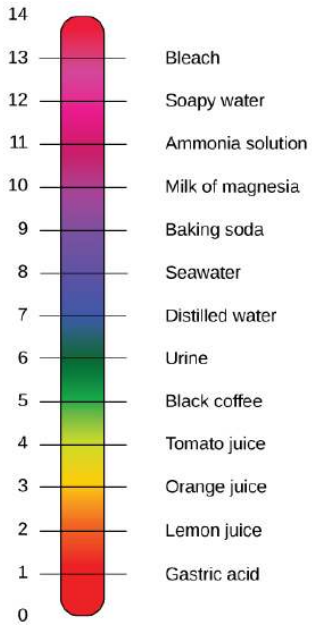


Figure **7.5.*b***: The pH scale measures the amount of hydrogen ions (H^+) in a substance. This shows the pH of common household solutions. Those with a pH greater than 7 are basic (alkaline), and those with a pH less than 7 are acidic. The solutions from high to low pH are bleach (13), soapy water (12), ammonia solution (11), milk of magnesia (10), baking soda (9), seawater (8), distilled water (7), urine (6), black coffee (5), tomato juice (4), orange juice (3), lemon juice (2), and gastric acid (1). Note that pH values are approximate. Image and caption (modified) from OpenStax/Edward Stevens (CC-BY). Access for free at openstax.org.

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 increasing leaching and lowering pH. 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%). 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.

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 **7.5.*c***). **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.

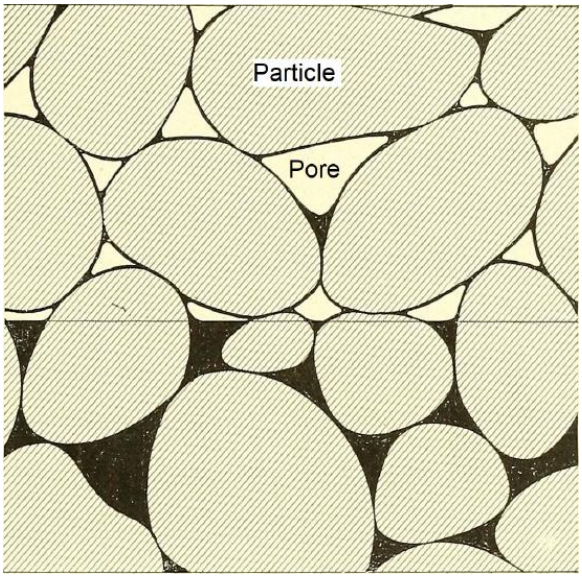


Figure **7.5.*c***: Soil particles and the pore spaces in between them. The black shading represents water, which fills the pore spaces in the lower portion of the soil and clings to narrow portions of pore space in the top portion of the soil. Image from "Forest physiography; physiography of the United States and principles of soils in relation to forestry" (public domain).

Soil texture is based on percentages of sand, silt, and clay (figure **7.5.*d***). 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.

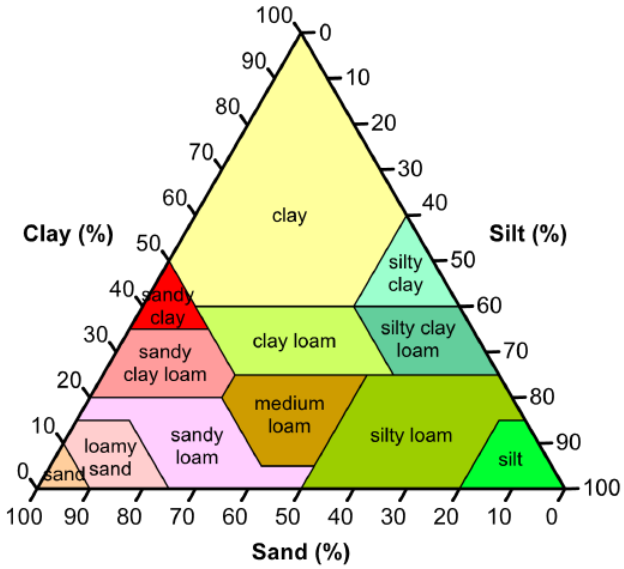


Figure **7.5.*d***: A soil texture triangle is used to determine the soil texture based on the percentages of sand, silt, and clay. The left axis represents the percentage of clay. The right axis represents the percentage of silt. The bottom axis represents the percentage of sand. Most soils that contain more than 40% 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. Image by Richard Wheeler/Zephyris at English Wikipedia (CC-BY-SA).

Organic Versus Mineral Soils

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 **7.5.*e***). **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 7.5.*e*): Decomposition of organic material occurs very slowly in this acidic bog. The organic material accumulates, which is characteristic of organic soils. Image by William L. Farr (CC-BY-SA).

Soil 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 7.5.*f*-g). 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 7.5.*f*), 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.

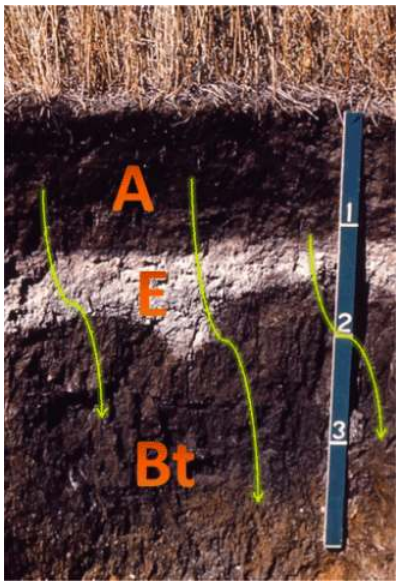


Figure 7.5.*f*): Soil Profile. Photograph shows a soil profile from South Dakota revealing three horizons. The A horizon (topsoil) is dark brown and extend about 1 foot. Below it is the white E (eluviated) horizon, which is about 6 inches thick. The B horizon (subsoil, labeled Bt) is the medium brown 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.

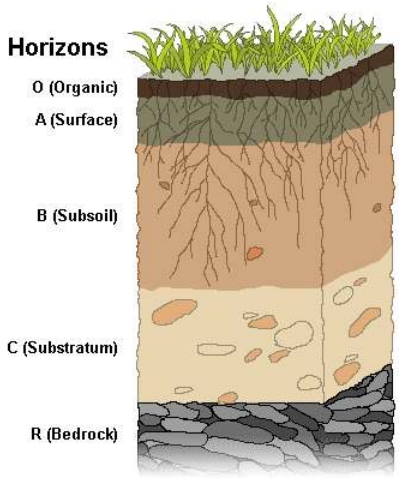


Figure 7.5.g): This image shows the different horizons, or layers, in soil. Vegetation grows at the surface. The top, deep brown layer is the O (organic) horizon. Below this is the gray A horizon (topsoil, or surface). Next is the light brown B horizon (subsoil). The C horizon (substratum, or soil base) 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. This work by Wilsonbiggs is licensed under CC BY-SA 4.0

O horizon

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

A horizon

The **A horizon** (topsoil) consists of a mixture of organic material with inorganic products of weathering, and it is therefore the beginning of true mineral soil. 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. 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. 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.

Factors Affecting 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. See the Biomes chapter for more details about the effect of climate on soils.

Ancient soils, sometimes buried and preserved in the subsurface, are referred to as **paleosols** (figure 7.5.*h*) and reflect past climatic and environmental conditions.

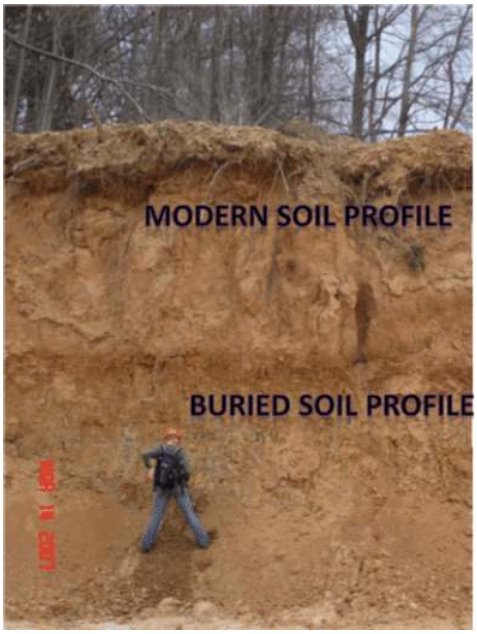


Figure 7.5.*h*: Modern versus Buried Soil Profiles. A buried soil profile, or paleosol (above geologist ‘s head), represents soil development during the last interglacial period. A modern soil profile (Alfisol) occurs near the land surface. Source: D. Grimley.

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 7.5.*i*). 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.

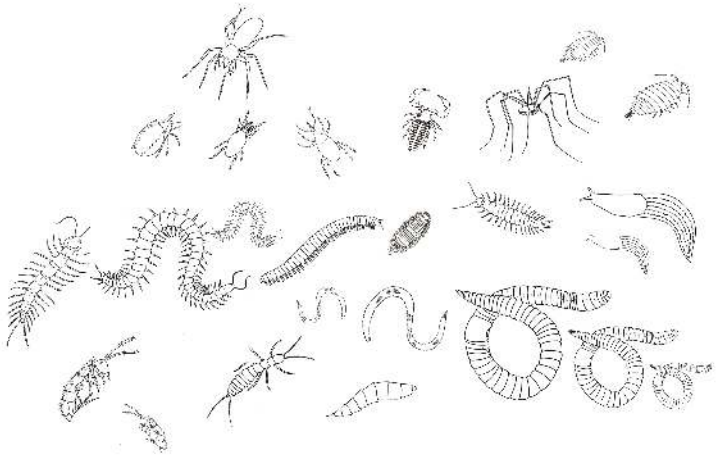


Figure 7.5.*i*: Illustration of animals commonly found in the soil. Image by Arne Hendriks (CC-BY)

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, for example, will take longer to develop. 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 **7.5.*j***).



Figure **7.5.*j***: 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. Image by Noah Elhardt (CC-BY).

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 Taxonomy

Soils are classified into one of 12 soil orders based on soil horizons, how they form, and their chemical compositions. For example, Mollisols (figure **7.5.*f***), 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.

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7.5.1: Soil Degradation

Once fertile topsoil is lost, it is not easily replaced. **Soil degradation** refers to deterioration in the quality of the soil and the resultant reduction in its capacity to produce. Soils are degraded primarily by erosion, compaction, and salinization. Such processes often arise from poor soil management during agricultural activities. In extreme cases, soil degradation can lead to **desertification** (conversion of land to desert-like conditions) of croplands and rangelands in semi-arid regions. See the Sustainable Agriculture section for strategies to preserve soil quality (**soil conservation**).

Erosion

Erosion is the biggest cause of soil degradation. Soil productivity is reduced as a result of losses of nutrients, water holding capacity, and organic matter. **Water holding capacity** is a measure of of the soils ability to retain water. The two agents of erosion are wind and water, which act to remove the finer particles from the soil. **Wind erosion** occurs mostly in flat, dry areas and moist, sandy areas along bodies of water. Wind not only removes soil, but also dries and degrades the soil structure. **Water erosion** is the most prevalent type of erosion. It occurs when raindrops splash on the ground and when water moves down slope as a thin film, small streams, or a large stream.

Some amount of soil erosion is a natural process along sloping areas and/or in areas with soft or materials that do not stick together and are susceptible to movement by water, wind, or gravity. For instance, soil material can be mobilized in strong windstorms, along the banks of rivers, in landslides, or by wave action along coastlines. However, human activities such as construction, logging, and off-road vehicle use promote erosion by removing the natural vegetation cover protecting the soil. Agricultural practices such as overgrazing and leaving plowed fields bare for extended periods contribute to farmland erosion. Each year, an estimated two billion metric tons of soil are eroded from farmlands in the United States alone. The soil transported by the erosion processes can also create problems elsewhere (for example, by clogging waterways and filling ditches and low-lying land areas). The areas most vulnerable to soil erosion include locations with thin organic (A and O) horizons and hilly terrains (figure **7.5.1.*a***).

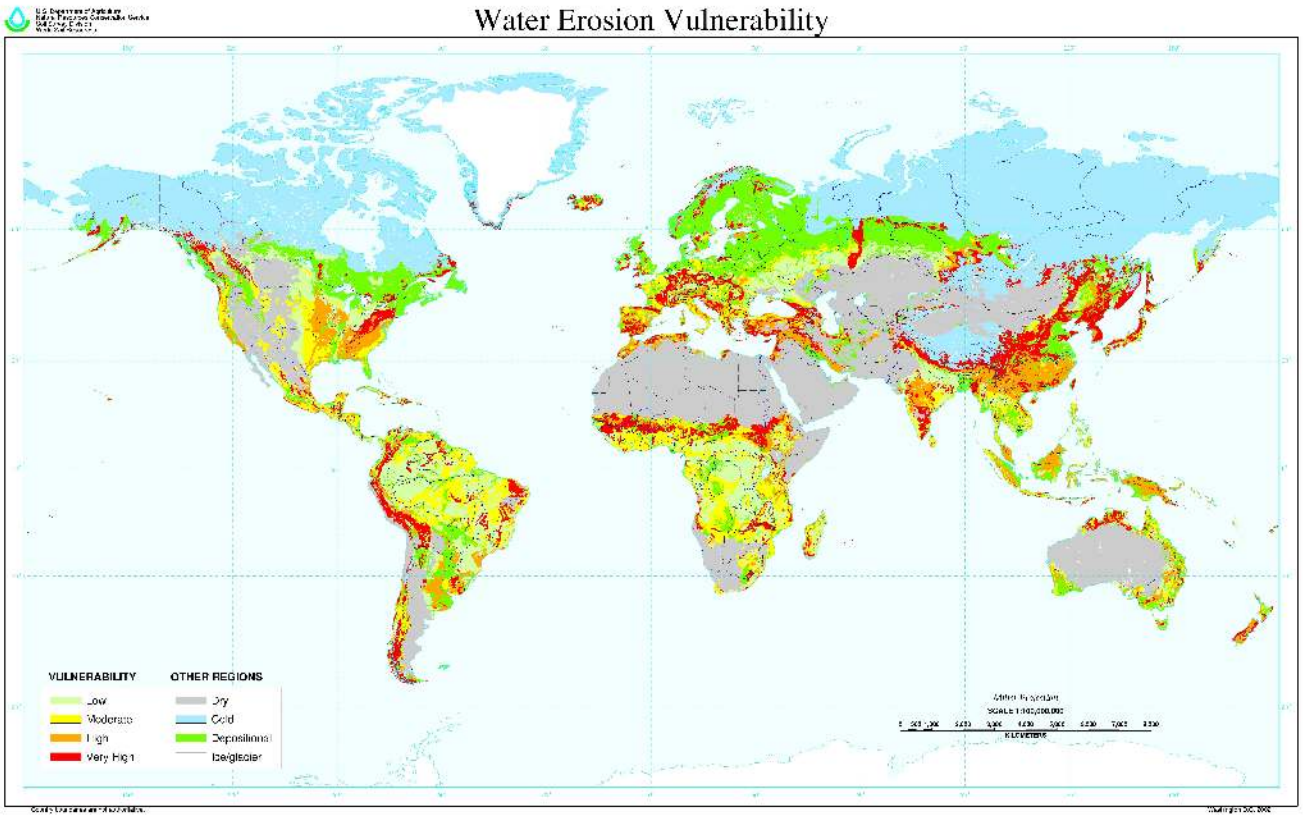


Figure 7.5.1.*a*: Global map of water erosion vulnerability. There are four levels of vulnerability: very high (red), high (orange), moderate (yellow), and low (light green). Examples of regions with very high vulnerability to erosion by water include the west coast of South America, parts of the eastern United States, regions around the Mediterranean Sea, a strip across western and central Africa, Korean and Japan, Northern Australia, and New Zealand. Examples of regions with low vulnerability include northern South America, the Democratic Republic of Congo, northern India and Nepal, and western Russia. Other regions are labeled as dry (gray), cold (light blue), depositional (bright green), or ice/glacier (white). For example, northern regions are cold and ice/glacier. Much of the western United States, Chile and Argentina, northern Africa, the Middle East, Kazakhstan, Mongolia, and much of Australia are considered dry. The largest depositional area (region where sediments accumulate) is northeastern Europe. Image by USDA-NRCS, Soil Science Division, World Soil Resources (public domain).

Compaction

In modern agricultural practices, heavy machinery is used to prepare the seedbed, for planting, to control weeds, and to harvest the crop. The use of heavy equipment has many advantages in saving time and labor, but can cause compaction of soil and disruption of the natural soil biota. Much compaction is reversible and some is unavoidable with modern practices; however, serious compaction issues can occur when the equipment is used excessively during times when the soil has a high water content. The problem with soil compaction is that increased soil density limits root penetration depth and may inhibit proper plant growth.

Salinization

When considerable quantities of salt accumulate in the soil in a process known as **salinization**, many plants are unable to grow properly or even survive. This is especially a problem in irrigated farmland. Groundwater used for irrigation contains small amounts of dissolved salts. Irrigation water that is not absorbed into the soil evaporates, leaving the salts behind. This process repeats itself and eventually severe salinization of the soil occurs. A related problem is water logging of the soil. When cropland is irrigated with excessive amounts of water in order to leach salts that have accumulated in the soil, the excess water is sometimes unable to drain away properly. In this case it accumulates underground and causes a rise in the subsurface water table. If the saline water rises to the level of the plant roots, plant growth is inhibited.

Desertification

Land that was previously suited for growing crops may be turned into desert by climate change and the activities of humans, such as poor farming practices, livestock overgrazing, and overuse of available water. This process, called **desertification**, is a serious problem worldwide. Plants and soil types that are non-arid (not dry) specifically help water soak into the ground (infiltration) and water retention. When desertification begins, it leads to a reduction in vegetation and degraded soil quality, and this further increases the aridity and spreads the desert via a **positive feedback loop** (meaning that the processes feed on themselves promoting an increasing spiral).

Figure **7.5.1.*b*** shows areas of the world and their vulnerability to desertification. Note the red and orange areas in the western and midwestern United States. The Dust Bowl of the 1930s is a classic example of human-caused desertification (figure **7.5.1.*c***). Poor cultivation and grazing practices -- coupled with severe drought conditions -- led to severe wind erosion of soil in a region of the Great Plains that became known as the "Dust Bowl". Wind stripped large areas of farmlands of topsoil, and formed clouds of dust that traveled as far as the eastern United States.

Sometimes there is a conflict between what is known to prevent desertification and what an individual farmer feels is needed to do to make a living. Mitigating the desertification process includes both societal steps and individual education on alternatives.

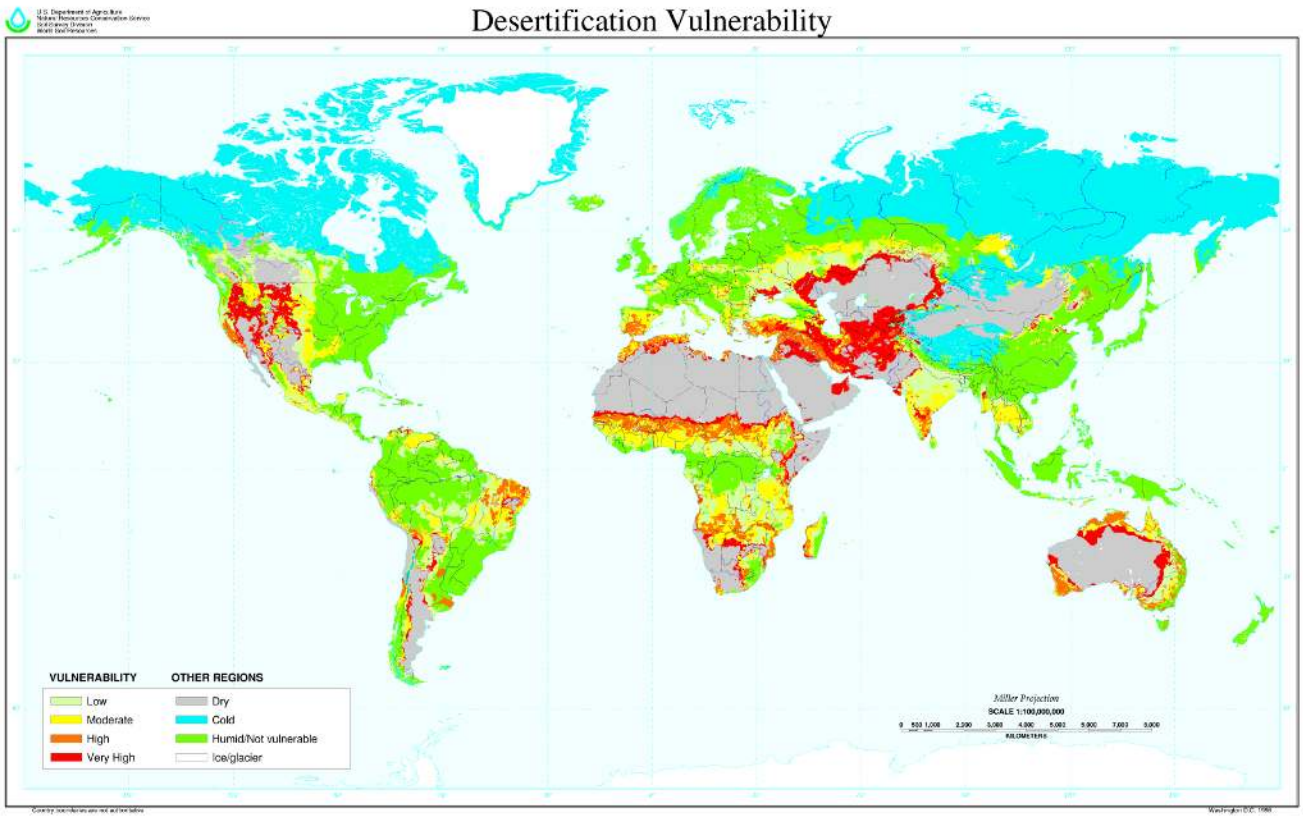


Figure **7.5.1.*b***: World map showing desertification vulnerability. There are four levels of vulnerability: very high (red), high (orange), moderate (yellow), and low (light green). Examples of regions with a very high vulnerability to desertification include the northwestern United States, a strip through western and central Africa, parts of the middle East, and parts of Australia. Examples of regions with low vulnerability include parts of Canada, parts of western Europe, and parts of Angola and the Democratic Republic of Congo. Other regions are labeled as dry (gray), cold (light blue), humid/not vulnerable (bright green), or ice/glacier (white). For example, northern regions are cold and ice/glacier. Some of southwestern United States, Chile and Argentina, northern Africa, the Middle East, Kazakhstan, Mongolia, and much of Australia are considered dry. Examples of humid/not vulnerable areas include the eastern United States, northern and eastern South America, western Europe, Central Africa, and East Asia. Image by USDA (public domain).



Figure **7.5.1.*c***: A cloud of dust in Kansas in 1935, part of the Dust Bowl. Image by NOAA Photo Library (public domain).

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7.6: KEY TERMS

acid rain
corrosive rain caused by rainwater falling to the ground through sulfur dioxide gas, turning it into weak sulfuric acid; can damage structures and ecosystems

analytical model
ecosystem model that is created with mathematical formulas to predict the effects of environmental disturbances on ecosystem structure and dynamics

apex consumer
organism at the top of the food chain

assimilation
biomass consumed and assimilated from the previous trophic level after accounting for the energy lost due to incomplete ingestion of food, energy used for respiration, and energy lost as waste

biogeochemical cycle
cycling of mineral nutrients through ecosystems and through the nonliving world

biomagnification
increasing concentrations of persistent, toxic substances in organisms at each trophic level, from the primary producers to the apex consumers

biomass
total weight, at the time of measurement, of living or previously living organisms in a unit area within a trophic level

chemoautotroph
organism capable of synthesizing its own food using energy from inorganic molecules

conceptual model
(also, compartment model) ecosystem model that consists of flow charts that show the interactions of different compartments of the living and nonliving components of the ecosystem

dead zone
area within an ecosystem in lakes and near the mouths of rivers where large areas of ecosystems 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

detrital food web
type of food web in which the primary consumers consist of decomposers; these are often associated with grazing food webs within the same ecosystem

ecological pyramid
(also, Eltonian pyramid) graphical representation of different trophic levels in an ecosystem based of organism numbers, biomass, or energy content

ecosystem
community of living organisms and their interactions with their abiotic environment

ecosystem dynamics
study of the changes in ecosystem structure caused by changes in the environment or internal forces

equilibrium
steady state of an ecosystem where all organisms are in balance with their environment and each other

eutrophication

process whereby nutrient runoff causes the excess growth of microorganisms, depleting dissolved oxygen levels and killing ecosystem fauna

fallout
direct deposit of solid minerals on land or in the ocean from the atmosphere

food chain
linear representation of a chain of primary producers, primary consumers, and higher-level consumers used to describe ecosystem structure and dynamics

food web
graphic representation of a holistic, nonlinear web of primary producers, primary consumers, and higher-level consumers used to describe ecosystem structure and dynamics

grazing food web
type of food web in which the primary producers are either plants on land or phytoplankton in the water; often associated with a detrital food web within the same ecosystem

gross primary productivity
rate at which photosynthetic primary producers incorporate energy from the sun

holistic ecosystem model
study that attempts to quantify the composition, interactions, and dynamics of entire ecosystems; often limited by economic and logistical difficulties, depending on the ecosystem

hydrosphere
area of the Earth where water movement and storage occurs

mesocosm
portion of a natural ecosystem to be used for experiments

microcosm
re-creation of natural ecosystems entirely in a laboratory environment to be used for experiments

net consumer productivity
energy content available to the organisms of the next trophic level

net primary productivity
energy that remains in the primary producers after accounting for the organisms' respiration and heat loss

net production efficiency (NPE)
measure of the ability of a trophic level to convert the energy it receives from the previous trophic level into biomass

nonrenewable resource
resource, such as fossil fuel, that is either regenerated very slowly or not at all

primary consumer
trophic level that obtains its energy from the primary producers of an ecosystem

primary producer
trophic level that obtains its energy from sunlight, inorganic chemicals, or dead and/or decaying organic material

residence time
measure of the average time an individual water molecule stays in a particular reservoir

resilience (ecological)
speed at which an ecosystem recovers equilibrium after being disturbed

resistance (ecological)
ability of an ecosystem to remain at equilibrium in spite of disturbances

secondary consumer
usually a carnivore that eats primary consumers

simulation model
ecosystem model that is created with computer programs to holistically model ecosystems and to predict the effects of environmental disturbances on ecosystem structure and dynamics

subduction
movement of one tectonic plate beneath another

tertiary consumer
carnivore that eats other carnivores

trophic level
position of a species or group of species in a food chain or a food web

trophic level transfer efficiency (TLTE)
energy transfer efficiency between two successive trophic levels

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7.7: CHAPTER SUMMARY

46.1 ECOLOGY OF ECOSYSTEMS

Ecosystems exist on land, at sea, in the air, and underground. Different ways of modeling ecosystems are necessary to understand how environmental disturbances will affect ecosystem structure and dynamics. Conceptual models are useful to show the general relationships between organisms and the flow of materials or energy between them. Analytical models are used to describe linear food chains, and simulation models work best with holistic food webs.

46.2 ENERGY FLOW THROUGH ECOSYSTEMS

Organisms in an ecosystem acquire energy in a variety of ways, which is transferred between trophic levels as the energy flows from the bottom to the top of the food web, with energy being lost at each transfer. The efficiency of these transfers is important for understanding the different behaviors and eating habits of warm-blooded versus cold-blooded animals. Modeling of ecosystem energy is best done with ecological pyramids of energy, although other ecological pyramids provide other vital information about ecosystem structure.

46.3 BIOGEOCHEMICAL CYCLES

Mineral nutrients are cycled through ecosystems and their environment. Of particular importance are water, carbon, nitrogen, phosphorus, and sulfur. All of these cycles have major impacts on ecosystem structure and function. A variety of human activities, such as pollution, oil spills, and other events have damaged ecosystems, potentially causing global climate change. The health of Earth depends on understanding these cycles and how to protect the environment from irreversible damage.

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7.8: VISUAL CONNECTION QUESTIONS

1.

Figure 46.8 Why do you think the value for gross productivity of the primary producers is the same as the value for total heat and respiration (20,810 kcal/m^2/yr)?

2.

Figure 46.10 Pyramids depicting the number of organisms or biomass may be inverted, upright, or even diamond-shaped. Energy pyramids, however, are always upright. Why?

3.

Figure 46.17 Which of the following statements about the nitrogen cycle is false?

1. Ammonification converts organic nitrogenous matter from living organisms into ammonium (NH_4^+).
2. Denitrification by bacteria converts nitrates (NO_3^-) to nitrogen gas (N_2).
3. Nitrification by bacteria converts nitrates (NO_3^-) to nitrites (NO_2^-).
4. Nitrogen fixing bacteria convert nitrogen gas (N_2) into organic compounds.

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7.9: REVIEW QUESTIONS

4.

The ability of an ecosystem to return to its equilibrium state after an environmental disturbance is called _____.

1. resistance
2. restoration
3. reformation
4. resilience

5.

A re-created ecosystem in a laboratory environment is known as a _____.

1. mesocosm
2. simulation
3. microcosm
4. reproduction

6.

Decomposers are associated with which class of food web?

1. grazing
2. detrital
3. inverted
4. aquatic

7.

The primary producers in an ocean grazing food web are usually _____.

1. plants
2. animals
3. fungi
4. phytoplankton

8.

What term describes the use of mathematical equations in the modeling of linear aspects of ecosystems?

1. analytical modeling
2. simulation modeling
3. conceptual modeling
4. individual-based modeling

9.

The position of an organism along a food chain is known as its _____.

1. locus
2. location
3. trophic level
4. microcosm

10.

The loss of an apex consumer would impact which trophic level of a food web?

1. primary producers
2. primary consumers
3. secondary consumers
4. all of the above

11.

A food chain would be a better resource than a food web to answer which question?

1. How does energy move from an organism in one trophic level to an organism on the next trophic level?
2. How does energy move within a trophic level?

3. What preys on grasses?
4. How is organic matter recycled in a forest?

12.

The weight of living organisms in an ecosystem at a particular point in time is called:

1. energy
2. production
3. entropy
4. biomass

13.

Which term describes the process whereby toxic substances increase along trophic levels of an ecosystem?

1. biomassification
2. biomagnification
3. bioentropy
4. heterotrophy

14.

Organisms that can make their own food using inorganic molecules are called:

1. autotrophs
2. heterotrophs
3. photoautotrophs
4. chemoautotrophs

15.

In the English Channel ecosystem, the number of primary producers is smaller than the number of primary consumers because_____.

1. the apex consumers have a low turnover rate
2. the primary producers have a low turnover rate
3. the primary producers have a high turnover rate
4. the primary consumers have a high turnover rate

16.

What law of chemistry determines how much energy can be transferred when it is converted from one form to another?

1. the first law of thermodynamics
2. the second law of thermodynamics
3. the conservation of matter
4. the conservation of energy

17.

The mussels that live at the NW Eifuku volcano are examples of _____.

1. chemoautotrophs
2. photoautotrophs
3. apex predators
4. primary consumers

18.

The movement of mineral nutrients through organisms and their environment is called a _____ cycle.

1. biological
2. bioaccumulation
3. biogeochemical
4. biochemical

19.

Carbon is present in the atmosphere as _____.

1. carbon dioxide
2. carbonate ion

3. carbon dust
4. carbon monoxide

20.

The majority of water found on Earth is:

1. ice
2. water vapor
3. fresh water
4. salt water

21.

The average time a molecule spends in its reservoir is known as _____.

1. residence time
2. restriction time
3. resilience time
4. storage time

22.

The process whereby oxygen is depleted by the growth of microorganisms due to excess nutrients in aquatic systems is called _____.

1. dead zoning
2. eutrophication
3. retrofication
4. depletion

23.

The process whereby nitrogen is brought into organic molecules is called _____.

1. nitrification
2. denitrification
3. nitrogen fixation
4. nitrogen cycling

24.

Which of the following approaches would be the most effective way to reduce greenhouse carbon dioxide?

1. Increase waste deposition into the deep ocean.
2. Plant more environmentally-suitable plants.
3. Increase use of fuel sources that do not produce carbon dioxide as a by-product.
4. Decrease livestock agriculture.

25.

How would loss of fungi in a forest effect biogeochemical cycles in the area?

1. Nitrogen could no longer be fixed into organic molecules.
2. Phosphorus stores would be released for use by other organisms.
3. Sulfur release from eroding rocks would cease.
4. Carbon would accumulate in dead organic matter and waste.

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7.10: CRITICAL THINKING QUESTIONS

26.

Compare and contrast food chains and food webs. What are the strengths of each concept in describing ecosystems?

27.

Describe freshwater, ocean, and terrestrial ecosystems.

28.

Compare grazing and detrital food webs. Why would they both be present in the same ecosystem?

29.

How does the microcosm modeling approach differ from utilizing a holistic model for ecological research?

30.

How do conceptual and analytical models of ecosystems complement each other?

31.

Compare the three types of ecological pyramids and how well they describe ecosystem structure. Identify which ones can be inverted and give an example of an inverted pyramid for each.

32.

How does the amount of food a warm-blooded animal (endotherm) eats relate to its net production efficiency (NPE)?

33.

A study uses an inverted pyramid to demonstrate the relationship between sharks, their aquatic prey, and phytoplankton in an ocean region. What type of pyramid must be used? What does this convey to readers about predation in the area?

34.

Describe what a pyramid of numbers would like if an ecologist models the relationship between bird parasites, blue jays, and oak trees in a hectare. Does this match the energy flow pyramid?

35.

Describe nitrogen fixation and why it is important to agriculture.

36.

What are the factors that cause dead zones? Describe eutrophication, in particular, as a cause.

37.

Why are drinking water supplies still a major concern for many countries?

38.

Discuss how the human disruption of the carbon cycle has caused ocean acidification.

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CHAPTER OVERVIEW

8: CONSERVATION BIOLOGY AND BIODIVERSITY

Conservation biology is the management of nature and of Earth's biodiversity with the aim of protecting species, their habitats, and ecosystems from excessive rates of extinction and the erosion of biotic interactions. It is an interdisciplinary subject drawing on natural and social sciences, and the practice of natural resource management.

8.1: Introduction
8.2: The Biodiversity Crisis
8.3: The Importance of Biodiversity to Human Life
8.4: Threats to Biodiversity
8.5: Preserving Biodiversity
8.6: Key Terms
8.7: Chapter Summary
8.8: Visual Connection Questions
8.9: Review Questions
8.10: Critical Thinking Questions

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8.1: INTRODUCTION



Figure 47.1 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)

CHAPTER OUTLINE

47.1 The Biodiversity Crisis
47.2 The Importance of Biodiversity to Human Life
47.3 Threats to Biodiversity
47.4 Preserving Biodiversity

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 is an enormous and deep 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. When they sampled for fish in different locations of the lake, the researchers identified over 500 evolved species in total. However, the scientists soon discovered that the invasive Nile Perch was destroying the lake's cichlid population, bringing hundreds of cichlid species to extinction with devastating rapidity.

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8.2: THE BIODIVERSITY CRISIS

LEARNING OBJECTIVES

By the end of this section, you will be able to do the following:

- Define biodiversity in terms of species diversity and abundance
- Describe biodiversity as the equilibrium of naturally fluctuating rates of extinction and speciation
- Identify historical causes of high extinction rates in Earth's history

Traditionally, ecologists have measured biodiversity, a general term for the number of species present in the biosphere, by taking into account both the number of species and their relative abundance to each other. Biodiversity can be estimated at a number of levels of organization of living organisms. These estimation indices, which came from *information theory*, are most useful as a first step in quantifying biodiversity between and within ecosystems; they are less useful when the main concern among conservation biologists is simply the loss of biodiversity. However, biologists recognize that measures of biodiversity, in terms of species diversity, may help focus efforts to preserve the biologically or technologically important elements of biodiversity.

The Lake Victoria cichlids provide an example with 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 specialized habitat types and specific feeding strategies: such as eating plankton floating in the water, scraping/eating algae from rocks, eating insect larvae from the lake bottom, and eating the eggs of other species of cichlid. The cichlids of Lake Victoria are the product of a complex *adaptive radiation*. An adaptive radiation is a rapid (less than three million years in the case of the Lake Victoria cichlids) branching through speciation of a phylogenetic clade into many closely related species. Typically, the species "radiate" into different habitats and niches. The Galápagos Island 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 formerly included about 500 species.

At the time biologists were making this discovery, some species began to quickly disappear. A culprit in these declines was the Nile perch, a species of large predatory 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 its populations did not begin to surge until the 1980s. The 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 catalogued 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 that is caused primarily 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: 1) destruction of habitat, 2) introduction of exotic species, and 3) 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 these extinctions were caused by cataclysmic events that changed the course of the history of life in each instance.

TYPES OF BIODIVERSITY

Scientists generally accept that the term biodiversity describes the number and kinds of species and their abundance in a given location or on the planet. 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. Biologists have also identified alternate measures of biodiversity, some of which are important for planning how to preserve biodiversity.

Genetic diversity is one of those alternate concepts. Genetic diversity, or genetic variation defines the raw material for evolution and adaptation in a species. A species' future potential for adaptation depends on the genetic diversity held in the genomes of the individuals in populations that make up the species. 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 are genetically similar 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.

Many genes code for proteins, which in turn carry out the metabolic processes that keep organisms alive and reproducing. Genetic diversity can be measured as chemical diversity in that different species produce a variety of chemicals in their cells, both the proteins as well as the products and byproducts of metabolism. This chemical diversity has potential benefit for humans as a source of pharmaceuticals, so it provides one way to measure diversity that is important to human health and welfare.

Humans have generated diversity in domestic animals, plants, and fungi, among many other organisms. This diversity is also suffering losses because of migration, market forces, and increasing globalism in agriculture, especially in densely populated regions such as China, India, and Japan. The human population directly depends on this diversity as a stable food source, and its decline is troubling biologists and agricultural scientists.

It is also useful to define ecosystem diversity, meaning the number of different ecosystems on the planet or within a given geographic area (Figure 47.2). 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 largely extinct ecosystem in North America is the *prairie ecosystem*. 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 species survive elsewhere, but the hugely productive ecosystem that was responsible for creating the most productive agricultural soils in the United States is now gone. As a consequence, native soils are disappearing or must be maintained and enhanced at great expense.



(a)



(b)

Figure 47.2 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)

CURRENT SPECIES DIVERSITY

Despite considerable effort, knowledge of the species that inhabit the planet is limited and always will be because of a continuing lack of financial resources and political willpower. A recent estimate suggests that the eukaryote species for which science has names, about 1.5 million species, account for less than 20 percent of the total number of eukaryote species present on the planet (8.7 million species, by one estimate). Estimates of numbers of prokaryotic species are largely guesses, but biologists agree that science has only begun to catalog their diversity. Even with what is known, there is no central repository of names or samples of the described species; therefore, there is no way to be sure that the 1.5 million descriptions *is* an accurate accounting. It is a best guess based on the opinions of experts in different taxonomic groups. Given that Earth is losing species at an accelerating pace, science is very much in the place it was with the Lake Victoria cichlids: knowing little about what is being lost. Table 47.1 presents recent estimates of biodiversity in different groups.

Estimates of the Numbers of Described and Predicted Species by Taxonomic Group

	Mora et al. 2011[1]		Chapman 2009[2]		Groombridge & Jenkins 2002[3]	
	Described	Predicted	Described	Predicted	Described	Predicted
Animalia	1,124,516	9,920,000	1,424,153	6,836,330	1,225,500	10,820,000
Chromista	17,892	34,900	25,044	200,500	—	—
Fungi	44,368	616,320	98,998	1,500,000	72,000	1,500,000
Plantae	224,244	314,600	310,129	390,800	270,000	320,000
Protozoa	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

Table 47.1

There are various initiatives to catalog described species in accessible ways, and the internet is facilitating that effort. Nevertheless, it has been pointed out that at the current rate of new species descriptions (which according to the State of Observed Species Report is 17,000 to 20,000 new species per year), it will take close to 500 years to finish describing life on this planet.[4] Over time, the task becomes both increasingly difficult and increasingly easier as extinction removes species from the planet.

Naming and counting species may seem like an unimportant pursuit given the other needs of humanity, but determining biodiversity it is not simply an accounting of species. Describing a species is a complex process through which biologists determine an organism's unique characteristics and whether or not that organism belongs to any other described species or genus. It allows biologists to find and recognize the species after the initial discovery, and allows them to follow up on questions about its biology. In addition, the unique characteristics of each species make it potentially valuable to humans or other species on which humans depend.

PATTERNS OF BIODIVERSITY

Biodiversity is not evenly distributed on Earth. Lake Victoria contained almost 500 species of cichlids alone, ignoring the other fish families present in the lake. All of these species were found only in Lake Victoria; therefore, the 500 species of cichlids were *endemic*. Endemic species are found in only one location. Endemics with highly restricted distributions are particularly vulnerable to extinction. Higher taxonomic levels, such as genera and families, can also be endemic. Lake Michigan contains about 79 species of fish, many of which are found in other lakes in North America. What accounts for the difference in fish diversity in these two lakes? Lake Victoria is an ancient tropical lake, while Lake Michigan is a recently formed temperate lake. Lake Michigan in its present form is only about 7,000 years old, while Lake Victoria in its present form is about 15,000 years old, although its basin is about 400,000 years in age. Biogeographers have suggested these two factors, latitude and age, are two of several hypotheses to explain biodiversity patterns on the planet.

CAREER CONNECTION

CAREER CONNECTION

BiogeographerBiogeography 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 environmental changes impact the distribution of a species; it has also been critical to developing modern evolutionary theory. Biogeographers need to understand both biology and ecology. They also need to be well-versed in evolutionary studies, soil science, and climatology.

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 known historical and current ecological information. Each of these fields considers both zoogeography and phytogeography—the past and present distribution of animals and plants.

One of the oldest observed patterns in ecology is that species biodiversity in almost every taxonomic group increases as latitude declines. In other words, biodiversity increases closer to the equator (Figure 47.3).

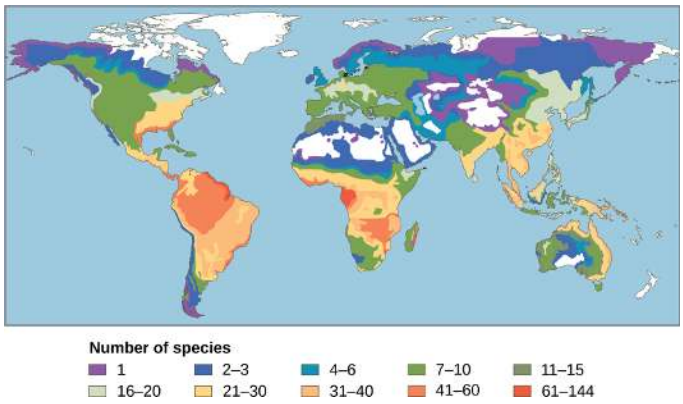


Figure 47.3 This map illustrates the number of amphibian species across the globe and shows the trend toward higher biodiversity at lower latitudes. A similar pattern is observed for most taxonomic groups. The white areas indicate a lack of data in this particular study.

It is not yet clear why biodiversity increases closer to the equator, but scientists have several hypotheses. One factor may be the greater age of the ecosystems in the tropics versus those in temperate regions; the temperate regions were largely devoid of life or were drastically reduced during the last glaciation. The idea is that greater age provides more time for speciation. Another possible explanation is the increased direct energy the tropics receive from the sun versus the decreased intensity of the solar energy that temperate and polar regions receive. Tropical ecosystem complexity may promote speciation by increasing the heterogeneity, or *number of ecological niches*, in the tropics relative to higher latitudes. The greater heterogeneity provides more opportunities for coevolution, specialization, and perhaps greater selection pressures leading to population differentiation. However, this hypothesis suffers from some circularity—ecosystems with more species encourage speciation, but how did they get more species to begin with?

The tropics have been perceived as being more stable than temperate regions, which have a pronounced climate and day-length seasonality. The tropics have their own forms of seasonality, such as rainfall, but they are generally assumed to be more stable environments and this stability might promote speciation into highly specialized niches.

Regardless of the mechanisms, it is certainly true that all levels of biodiversity are greatest in the tropics. Additionally, the *rate of endemism* is highest, and there are more biodiversity "hotspots." However, this richness of diversity also means that knowledge of species is unfortunately very low, and there is a high potential for biodiversity loss.

CONSERVATION OF BIODIVERSITY

In 1988, British environmentalist Norman Myers developed a conservation concept to identify areas rich in species and at significant risk for species loss: *biodiversity hotspots*. Biodiversity 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. By protecting hotspots, governments are able to protect a larger number of species. The original criteria for a hotspot included the presence of 1500 or more endemic plant species and 70 percent of the area disturbed by human activity. There are now 34 biodiversity hotspots (Figure 47.4) containing large numbers of endemic species, which include half of Earth's endemic plants.

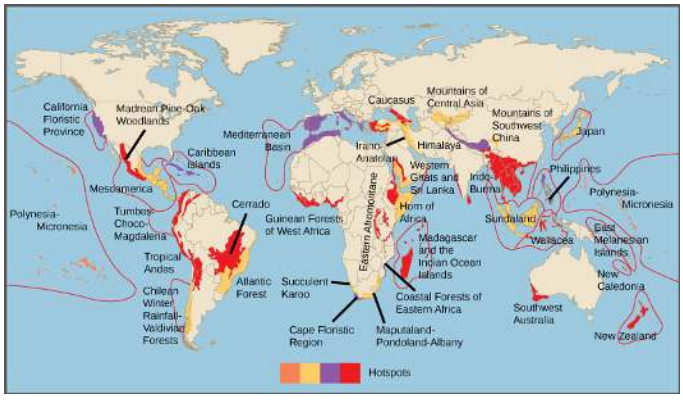


Figure 47.4 Conservation International has identified 34 biodiversity hotspots, which cover only 2.3 percent of the Earth's surface but have endemic to them 42 percent of the terrestrial vertebrate species and 50 percent of the world's plants.

BIODIVERSITY CHANGE THROUGH GEOLOGICAL TIME

The number of species on the planet, or in any geographical area, is the result of an equilibrium of two evolutionary processes that are continuously ongoing: *speciation* and *extinction*. Both are natural "birth" and "death" processes of macroevolution. When speciation rates begin to outstrip extinction rates, the number of species will increase; likewise, the number of species will decrease when extinction rates begin to overtake speciation rates. Throughout Earth's history, these two processes have fluctuated—sometimes leading to dramatic changes in the number of species on Earth as reflected in the fossil record (Figure 47.5).

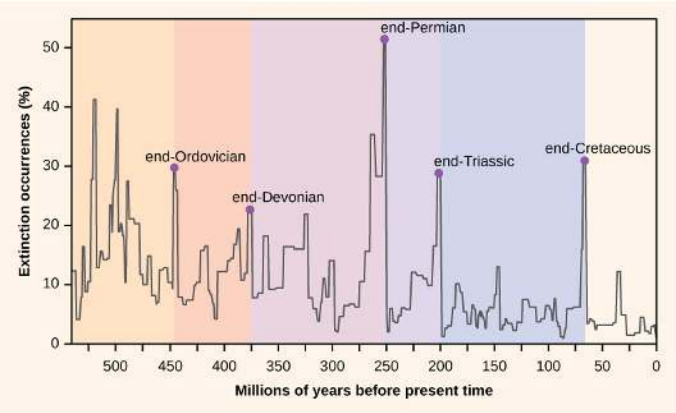


Figure 47.5 Percent extinction occurrences as reflected in the fossil record have fluctuated throughout Earth's history. Sudden and dramatic losses of biodiversity, called *mass extinctions*, have occurred five times.

Paleontologists have identified five strata in the fossil record that appear to show sudden and dramatic (greater than half of all extant species disappearing from the fossil record) losses in biodiversity. These are called mass extinctions. There are many lesser, yet still dramatic, extinction events, but the five mass extinctions have attracted the most research. An argument can be made that the five mass extinctions are only the five most *extreme events* in a continuous series of large extinction events throughout the Phanerozoic (since 542 million years ago). In most cases, the hypothesized causes are still controversial; however, the most recent mass extinction event seems clear.

THE FIVE MASS EXTINCTIONS

The fossil record of the mass extinctions was the basis for defining periods of geological history, so they typically occur at the transition point between geological periods. The transition in fossils from one period to another reflects the dramatic loss of species and the gradual origin of new species. These transitions can be seen in the rock strata. Table 47.2 provides data on the five mass extinctions.

Mass Extinctions

Geological Period	Mass Extinction Name	Time (millions of years ago)
Ordovician–Silurian	end-Ordovician O–S	450–440
Late Devonian	end-Devonian	375–360
Permian–Triassic	end-Permian	251
Triassic–Jurassic	end-Triassic	205
Cretaceous–Paleogene	end-Cretaceous K–Pg (K–T)	65.5

Table 47.2 This table shows the names and dates for the five mass extinctions in Earth's history.

The Ordovician-Silurian extinction event is the first recorded mass extinction and the second largest. During this period, about 85 percent of marine species (few species lived outside the oceans) became extinct. The main hypothesis for its cause is a period of glaciation and then warming. The extinction event actually consists of two extinction events separated by about 1 million years. The first event was caused by cooling, and the second event was due to the subsequent warming. The climate changes affected temperatures and sea levels. Some researchers have suggested that a gamma-ray burst, caused by a nearby supernova, was a possible cause of the Ordovician-Silurian extinction. The gamma-ray burst would have stripped away the Earth's protective ozone layer, allowing intense ultraviolet radiation from the sun to reach the surface of the earth—and *may* account for climate changes observed at the time. The hypothesis is very speculative, and extraterrestrial influences on Earth's history are an active line of research. Recovery of biodiversity after the mass extinction took from 5 to 20 million years, depending on the location.

The late Devonian extinction may have occurred over a relatively long period of time. It appears to have mostly affected marine species and not so much the plants or animals inhabiting terrestrial habitats. The causes of this extinction are poorly understood.

The end-Permian extinction was the largest in the history of life. Indeed, an argument could be made that Earth became nearly devoid of life during this extinction event. Estimates are that 96 percent of all marine species and 70 percent of all terrestrial species were lost. It was at

this time, for example, that the trilobites, a group that survived the Ordovician–Silurian extinction, became extinct. The causes for this mass extinction are not clear, but the leading suspect is extended and widespread volcanic activity that led to a runaway global-warming event. The oceans became largely anoxic, suffocating marine life. Terrestrial tetrapod diversity took 30 million years to recover after the end-Permian extinction. The Permian extinction dramatically altered Earth's biodiversity makeup and the course of evolution.

The causes of the Triassic–Jurassic extinction event are not clear, and researchers argue hypotheses including climate change, asteroid impact, and volcanic eruptions. The extinction event occurred just before the breakup of the supercontinent Pangaea, although recent scholarship suggests that the extinctions may have occurred more gradually throughout the Triassic.

The causes of the end-Cretaceous extinction event are the ones that are best understood. It was during this extinction event about 65 million years ago that the majority of the dinosaurs, the dominant vertebrate group for millions of years, disappeared from the planet (with the exception of a theropod clade that gave rise to birds).

The cause of this extinction is now understood to be the result of a cataclysmic impact of a large meteorite, or asteroid, off the coast of what is now the Yucatán Peninsula. This hypothesis, proposed first in 1980, was a radical explanation based on a sharp spike in the levels of *iridium* (which enters our atmosphere from meteors at a fairly constant rate but is otherwise absent on Earth's surface) in the rock stratum that marks the boundary between the Cretaceous and Paleogene periods (Figure 47.6). This boundary marked the disappearance of the dinosaurs in fossils as well as many other taxa. The researchers who discovered the iridium spike interpreted it as a rapid influx of iridium from space to the atmosphere (in the form of a large asteroid) rather than a slowing in the deposition of sediments during that period. It was a radical explanation, but the report of an appropriately aged and sized impact crater in 1991 made the hypothesis more believable. Now an abundance of geological evidence supports the theory. Recovery times for biodiversity after the end-Cretaceous extinction are shorter, in geological time, than for the end-Permian extinction, on the order of 10 million years.

Another possibility, perhaps coincidental with the impact of the Yucatan asteroid, was extensive volcanism that began forming about 66 million years ago, about the same time as the Yucatan asteroid impact, at the end of the Cretaceous. The lava flows covered over 50 percent of what is now India. The release of volcanic gases, particularly sulfur dioxide, during the formation of the traps contributed to climate change, which may have induced the mass extinction.

VISUAL CONNECTION

VISUAL CONNECTION



Figure 47.6 In 1980, Luis and Walter Alvarez, Frank Asaro, and Helen Michels discovered, across the world, a spike in the concentration of iridium within the sedimentary layer at the K–Pg boundary. These researchers hypothesized that this iridium spike was caused by an asteroid impact that resulted in the K–Pg mass extinction. In the photo, the iridium layer is the light band. (credit: USGS)

Scientists measured the relative abundance of fern spores above and below the K–Pg boundary in this rock sample. Which of the following statements most likely represents their findings?

1. An abundance of fern spores from several species was found below the K–Pg boundary, but none was found above.
2. An abundance of fern spores from several species was found above the K–Pg boundary, but none was found below.
3. An abundance of fern spores was found both above and below the K–Pg boundary, but only one species was found below the boundary, and many species were found above the boundary.
4. Many species of fern spores were found both above and below the boundary, but the total number of spores was greater below the boundary.

LINK TO LEARNING

LINK TO LEARNING

Explore this interactive website about mass extinctions.

THE PLEISTOCENE EXTINCTION

The Pleistocene Extinction is one of the lesser extinctions, and a recent one. It is well known that the North American, and to some degree Eurasian, megafauna—large vertebrate animals—disappeared toward the end of the last glaciation period. The extinction appears to have happened in a relatively restricted time period of 10,000–12,000 years ago. In North America, the losses were quite dramatic and included the woolly mammoths (with an extant population existing until about 4,000 years ago in isolation on Wrangel Island, Canada), mastodon, giant beavers, giant ground sloths, saber-toothed cats, and the North American camel, just to name a few. In the early 1900s, scientists first suggested the possibility that over-hunting caused the rapid extinction of these large animals. Research into this hypothesis continues today.

In general, the timing of the Pleistocene extinctions correlated with the arrival of paleo-humans, perhaps as long as 40,000 years ago, and not with climate-change events, which is the main competing hypothesis for these extinctions. The extinctions began in Australia about 40,000 to 50,000 years ago, just after the arrival of humans in the area: a marsupial lion, a giant one-ton wombat, and several giant kangaroo species disappeared. In North America, the extinctions of almost all of the large mammals occurred 10,000–12,000 years ago. All that are left are the smaller mammals such as bears, elk, moose, and cougars. Finally, on many remote oceanic islands, the extinctions of many species occurred coincidentally with human arrivals. Not all of the islands had large animals, but when there were large animals, they were often forced into extinction. Madagascar was colonized about 2,000 years ago and the large mammals that lived there became extinct. Eurasia and Africa do not show this pattern, but they also did not experience a recent arrival of hunter-gatherer humans. Rather, humans arrived in Eurasia hundreds of thousands of years ago. This topic remains an area of active research and hypothesizing. It seems clear that even if climate played a role, in most cases human hunting precipitated the extinctions.

RECENT EXTINCTIONS

The sixth, or Holocene, mass extinction appears to have begun earlier than previously believed and is largely due to the disruptive activities of modern *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.

One of the earlier and popularly known examples is the dodo bird. The odd pigeon-like bird lived in the forests of Mauritius (an island in the Indian Ocean) and became extinct around 1662. The dodo was hunted for its meat by sailors and was easy prey because it approached people without fear (the dodo had not evolved with humans). Pigs, rats, and dogs brought to the island by European ships also killed dodo young and eggs.

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 overhunted for meat and oil. The last sea cow was killed in 1768. That amounts to just 27 years between the sea cow’s first contact with Europeans and extinction of the species!

Since 1900, a variety of species have gone extinct, including the following:

- 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 overhunted and suffered from habitat loss that resulted from the clearing of forests for farmland.
- The Carolina parakeet, once common in the eastern United States, died out in 1918. It suffered habitat loss and was hunted to prevent it from eating orchard fruit. (The parakeet ate orchard fruit because 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 International Union for Conservation of Nature (IUCN) keeps a list of extinct and endangered species called the Red List. The list is not complete, but it describes 380 extinct species of vertebrates after 1500 AD, 86 of which were driven extinct by overhunting or overfishing.

ESTIMATES OF PRESENT-TIME EXTINCTION RATES

Estimates of extinction rates are hampered by the fact that most extinctions are probably happening without observation. The extinction of a bird or mammal is likely to be noticed by humans, especially if it has been hunted or used in some other way. But there are many organisms that are of less interest to humans (not necessarily of less value) and many that are undescribed.

The background extinction rate is estimated to be about one per million species per year (E/MSY). For example, assuming there are about ten million species in existence, the expectation is that ten species would become extinct each year (each year represents ten million species per year).

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. However, this value may be an underestimate for three reasons. First, many species would not have been described until much later in the time period, so their loss would have gone unnoticed. Second, the number of recently extinct vertebrate species is increasing because extinct species now are being described from skeletal remains. 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 closer to 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 by 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. Studies have shown that the number of species present increases as the size of the island increases. This phenomenon has also been shown to hold true in other island-like habitats as well, such as the mountain-top tepuis of Venezuela, which are surrounded by tropical forest. Turning this relationship around, if the habitat area is reduced, the number of species living there will also decline. Estimates of extinction rates based on habitat loss and species-area relationships have suggested that with about 90 percent habitat loss an expected 50 percent of species would become extinct. Species-area estimates have led to species extinction rate calculations of about 1000 E/MSY and higher. In general, actual observations do not show this amount of loss and suggestions have been made that there is a delay in extinction. Recent work has also called into question the applicability of the species-area relationship when estimating the loss of species. This work argues that the species-area relationship leads to an *overestimate* of extinction rates. A better relationship to use may be the endemics-area relationship. Using this method would bring estimates down to around 500 E/MSY in the coming century. *Note that this value is still 500 times the background rate*.

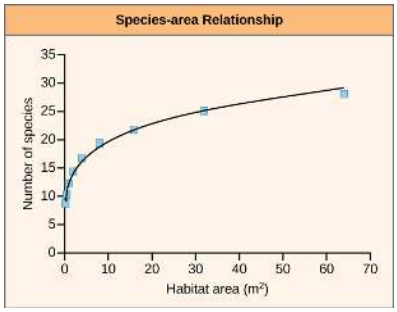


Figure 47.7 Studies have shown that the number of species present increases with the size of the habitat. (credit: modification of work by Adam B. Smith)

LINK TO LEARNING

LINK TO LEARNING

Check out this interactive exploration of endangered and extinct species, their ecosystems, and the causes of the endangerment or extinction.

FOOTNOTES

- 1Mora Camilo et al., "How Many Species Are There on Earth and in the Ocean?" *PLoS Biology* (2011), doi:10.1371/journal.pbio.1001127.
- 2Arthur D. Chapman, *Numbers of Living Species in Australia and the World*, 2nd ed. (Canberra, AU: Australian Biological Resources Study, 2009). www.environment.gov.au/system/files/pages/2ee3f4a1-f130-465b-9c7a-79373680a067/files/nlsaw-2nd-complete.pdf/.
- 3Brian Groombridge and Martin D. Jenkins. *World Atlas of Biodiversity: Earth's Living Resources in the 21st Century*. Berkeley: University of California Press, 2002.
- 4International Institute for Species Exploration (IISE), *2011 State of Observed Species (SOS)*. Tempe, AZ: IISE, 2011. Accessed May, 20, 2012. http://www.esf.edu/species/.

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8.3: THE IMPORTANCE OF BIODIVERSITY TO HUMAN LIFE

LEARNING OBJECTIVES

By the end of this section, you will be able to do the following:

- Identify chemical diversity benefits to humans
- Identify biodiversity components that support human agriculture
- Describe ecosystem services

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. But is the loss practically important for the welfare of the human species? From the perspective of evolution and ecology, the loss of a particular individual species is unimportant (however, we should note that the loss of a keystone species can lead to ecological disaster). Extinction is a normal part of macroevolution. But the *accelerated extinction rate* translates into the loss of tens of thousands of species within our lifetimes, and it is likely to have dramatic effects on human welfare through the collapse of ecosystems and in added costs to maintain food production, clean air and water, and human health.

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 humans to recognize their dependence on undomesticated living things on the planet. Biologists recognize the human species is embedded in ecosystems and is dependent on them, just as every other species on the planet is dependent. Technology smooths out the extremes of existence, but ultimately the human species cannot exist without a supportive ecosystem.

HUMAN HEALTH

Archeological evidence indicates that humans have been using plants for medicinal uses for thousands of years. A Chinese document from approximately 2800 BC is believed to be the first written account of herbal remedies, and such references occur throughout the global historical record. Contemporary indigenous societies that live close to the land often retain broad knowledge of the medicinal uses of plants growing in their area. Most plants produce secondary plant compounds, which are toxins used to protect the plant from insects and other animals that eat them, but some of which also work as medication.

Modern pharmaceutical science also recognizes the importance of these plant compounds. Examples of significant medicines derived from plant compounds include aspirin, codeine, digoxin, atropine, and vincristine (Figure 47.8). Many medicines 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. Antibiotics, which are responsible for extraordinary improvements in health and lifespans in developed countries, are compounds largely derived from fungi and bacteria.



Figure 47.8 *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 medicines improve people's lives. Pharmaceutical companies are always looking for new compounds synthesized by living organisms that can function as medicines. It is estimated that 1/3 of pharmaceutical research and development is spent on natural compounds and that about 35 percent of new drugs brought to market between 1981 and 2002 were derived from natural compounds. The opportunities for new medications will be reduced in direct proportion to the disappearance of species.

AGRICULTURAL DIVERSITY

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. Even the Inca capital of Machu Picchu had numerous gardens growing varieties of potatoes. 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 also demonstrates risks of low crop diversity. The tragic Irish potato famine occurred when the single variety grown in Ireland became susceptible to a potato blight, wiping out the entire crop. The loss of the potato crop led to mass famine and the related deaths of over one million people, as well as mass emigration of nearly two million people.

Disease resistance is a chief benefit of crop biodiversity, and 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 of maintaining 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 47.9) 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. 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.

VISUAL CONNECTION

VISUAL CONNECTION



Figure 47.9 The Svalbard Global Seed Vault is a storage facility for seeds of Earth's diverse crops. (credit: Mari Tefre, Svalbard Global Seed Vault)

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?

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.

Plant pollination is another key ecosystem service, provided by various species of bees, other insects, and birds. One estimate indicates that honey bee pollination provides the United States a $1.6 billion annual benefit.

Honey bee populations in North America have been suffering large losses caused by a syndrome known as colony collapse disorder, whose cause is unclear. (Evidence suggests the possible culprits may be the invasive varroa mite coupled with the Nosema gut parasite and acute paralysis virus.) Loss of these species would render it very difficult, if not impossible, to grow any of the 150 United States crops requiring pollination, including grapes, oranges, lemons, peppers, most brassica (broccoli and cauliflower), and many berries, melons, and nuts.

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 and evolve. 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.

WILD FOOD SOURCES

In addition to growing crops and raising animals for food, humans obtain food resources from wild populations, primarily fish populations. In fact, for approximately 1 billion people worldwide, aquatic resources provide the main source of animal protein. But since 1990, global fish production has declined, sometimes dramatically. Unfortunately, and despite considerable effort, few fisheries on the planet are managed for 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 the 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 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 as larger species are fished to extinction. The ultimate outcome could clearly be the loss of aquatic systems as food sources.

LINK TO LEARNING

LINK TO LEARNING

View a brief video discussing declining fish stocks.

PSYCHOLOGICAL AND MORAL VALUE

Finally, it has been clearly shown that humans benefit psychologically from living in a biodiverse world. A chief proponent of this idea is Harvard entomologist E. O. Wilson. He argues that human evolutionary history has adapted us to live in a natural environment and that city environments generate psychological stressors that affect human health and well-being. There is considerable research into the psychological regenerative benefits of natural landscapes that suggests 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.

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8.4: THREATS TO BIODIVERSITY

LEARNING OBJECTIVES

By the end of this section, you will be able to do the following:

- Identify significant threats to biodiversity
- Explain the effects of habitat loss, the introduction of exotic species, and hunting on biodiversity
- Identify the early and predicted effects of climate change on biodiversity

The core threat to biodiversity on the planet, and therefore a threat to human welfare, is the combination of human population growth and resource exploitation. The human population requires resources to survive and grow, and those resources are being removed unsustainably from the environment. The three greatest proximate threats to biodiversity are habitat loss, overharvesting, and the introduction of exotic species. The first two of these are a direct result of human population growth and resource use. The third results from increased mobility and trade. A fourth major cause of extinction, anthropogenic climate change, has not yet had a large impact, but it is predicted to become significant during this century. Global climate change is also a consequence of human population needs for energy and the use of fossil fuels to meet those needs (Figure 47.10). Environmental issues, such as toxic pollution, have specific targeted effects on species, but they are not generally seen as threats at the magnitude of the others.

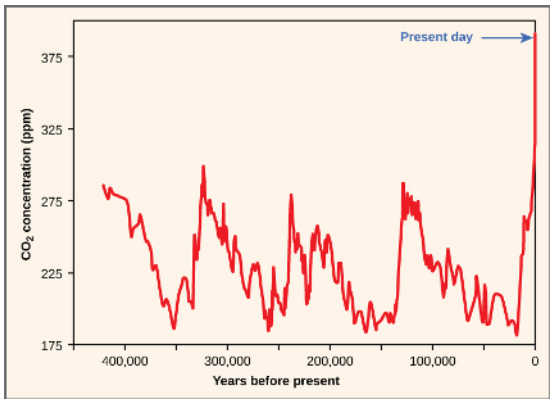


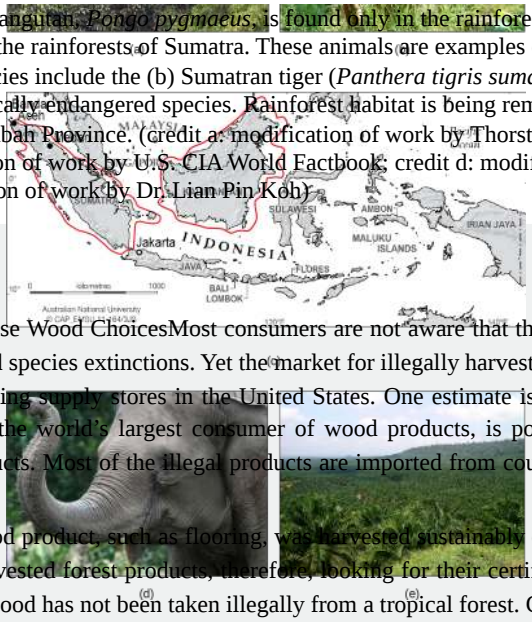
Figure 47.10 Atmospheric carbon dioxide levels fluctuate in a cyclical manner. However, the burning of fossil fuels in recent history has caused a dramatic increase in the levels of carbon dioxide in the Earth's atmosphere, which have now reached levels never before seen in human history. Scientists predict that the addition of this "greenhouse gas" to the atmosphere is resulting in climate change that will significantly impact biodiversity in the coming century.

HABITAT LOSS

Humans rely on technology to modify their environment and replace certain functions that were once performed by the natural ecosystem. Other species cannot do this. Elimination of their ecosystem—whether it is a forest, a desert, a grassland, a freshwater estuarine, or a marine environment—will kill the individuals belonging to the species. The species will become extinct if we remove the entire habitat within the range of a species. 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. All three species of orangutan are now listed as endangered by the International Union for Conservation of Nature (IUCN), but they are simply the most visible of thousands of species that will not survive the disappearance of the forests in Sumatra and Borneo. The forests are removed for timber and to plant palm oil plantations (Figure 47.11). Palm oil is used in many products including food products, cosmetics, and biodiesel in Europe. A five-year estimate of global forest cover loss for the years 2000–2005 was 3.1 percent. In the humid tropics where forest loss is primarily from timber extraction, 272,000 km^2 was lost out of a global total of 11,564,000 km^2 (or 2.4 percent). In the tropics, these losses certainly also represent the extinction of species because of high levels of endemism—species unique to a defined geographic location, and found nowhere else.



Figure 47.11 (a) One of three species of orangutan, *Pongo pygmaeus*, is found only in the rainforests of Borneo, and another 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)



EVERYDAY CONNECTION

EVERYDAY CONNECTION

Preventing Habitat Destruction with Wise Wood ChoicesMost consumers are not aware 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 in the United States. One estimate is that 10 percent of the imported timber stream in the United States, which is the world's largest consumer of wood products, is potentially illegally logged. In 2006, this amounted to $3.6 billion in wood products. Most of the illegal products are imported from countries that act as *intermediaries* and are not the originators of the wood.

How is it possible to determine if a wood product, such as flooring, was harvested sustainably or even legally? The Forest Stewardship Council (FSC) certifies sustainably harvested forest products, therefore, looking for their certification on flooring and other hardwood products is one way to ensure that the wood has not been taken illegally from a tropical forest. Certification applies to specific products, not to a producer; some producers' products may not have certification while other products are certified. While there are other industry-backed certifications other than the FSC, these are unreliable due to lack of independence from the industry. Another approach is to buy domestic wood species. While it would be great if there was a list of legal versus illegal wood products, 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 maintained sustainably all factor into whether a wood product will be certified by the FSC. If you are in doubt, 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 that are frequently modified through land development, damming, channelizing, or water removal. Damming affects the water flow to all parts of a river, which can reduce or eliminate populations that had adapted to the natural flow of the river. For example, an estimated 91 percent of United States rivers have been altered in some way. Modifications include dams, to create energy or store water; levees, to prevent flooding; and dredging or rerouting, to create land that is more suitable for human development. Many fish and amphibian species and numerous freshwater clams in the United States have seen declines caused by river damming and habitat loss. Habitat destruction, even when undertaken on behalf of humans, can lead to negative effects for us as well. Excessive soil erosion after forest removal, for example, can remove fertile soil and make river water toxic. Scientists and conservationists such as Wangari Maathai, who founded the Green Belt movement in Kenya, focus on replanting trees to repair habitats and prevent damage from deforestation. Maathai was awarded a Nobel Prize for her work, but unfortunately passed away in 2011.

OVERHARVESTING

Overharvesting is a serious threat to many species, but particularly to aquatic (both marine and freshwater) species. Despite regulation and monitoring, there are recent examples of fishery collapse. The western Atlantic cod fishery is the among the most significant. While it was a hugely productive fishery for 400 years, the introduction of modern factory trawlers in the 1980s caused it to become unsustainable. Fisheries collapse as a result of both economic and political factors. Fisheries are managed as a shared international resource even when the fishing territory lies within an individual country's territorial waters. Common resources are subject to an economic pressure known as the tragedy of the commons, in which essentially no fisher has a motivation to exercise restraint in harvesting a fishery when it is not owned by that fisher. Overexploitation is a common outcome. 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 always drive toward fishing the population to extinction.

LINK TO LEARNING

LINK TO LEARNING

Explore a U.S. Fish & Wildlife Service interactive map of critical habitat for endangered and threatened species in the United States. To begin, select "Visit the online mapper."

For the most part, fishery extinction is not equivalent to biological extinction—the last fish of a species is rarely fished out of the ocean. At the same time, fishery extinction is still harmful to fish species and their ecosystems. There are some instances in which true extinction is a possibility. Whales have slow-growing populations due to low reproductive rates, and therefore are at risk of complete extinction through hunting. There are some species of sharks with restricted distributions that are at risk of extinction. The groupers are another population of generally slow-growing fishes that, in the Caribbean, includes a number of species that are at risk of extinction from overfishing.

Coral reefs are extremely diverse marine ecosystems that face immediate 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 1 percent of marine habitat. Most home marine aquaria are stocked with wild-caught organisms, not cultured organisms. Although no species is known to have been driven extinct by the pet trade in marine species, 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 concerns about the effect of the pet trade on some terrestrial species such as turtles, amphibians, birds, plants, and even the orangutan.

LINK TO LEARNING

LINK TO LEARNING

View a brief video discussing the role of marine ecosystems in supporting human welfare and the decline of ocean ecosystems.

Bush meat is the generic term used for wild animals killed for food. Hunting is practiced throughout the world, but hunting practices, particularly in equatorial Africa and parts of Asia, are believed to threaten a number of species with extinction. Traditionally, bush meat in Africa was hunted to feed families directly; however, recent commercialization of the practice now has bush 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 bush meat trade are mostly mammals including many primates living in the Congo basin.

EXOTIC SPECIES

Exotic species are species that have been intentionally or unintentionally introduced into an ecosystem in which they did not evolve. For example, Kudzu (*Pueraria lobata*), which is native to Japan, was introduced in the United States in 1876. It was later planted for soil conservation. Problematically, it grows too well in the southeastern United States—up to a foot a day. It is now an invasive pest species and covers over 7 million acres in the southeastern United States. If an introduced species is able to survive in its new habitat, that introduction is now reflected in the observed range of the species. Human transportation of people and goods, including the intentional transport of organisms for trade, has dramatically increased the introduction of species into new ecosystems, sometimes at distances that are well beyond the capacity of the species to ever travel itself and outside the range of the species' natural predators.

Most exotic species introductions probably fail because of the low number of individuals introduced or poor adaptation to the ecosystem they enter. Some species, however, possess pre-adaptations that can make them especially successful in a new ecosystem. These exotic species often undergo dramatic population increases in their new habitat and reset the ecological conditions in the new environment, threatening the species that exist there. For this reason, exotic species are also called invasive species. Exotic species can threaten other species through competition for resources, predation, or disease. For example, the Eurasian star thistle, also called spotted knapweed, has invaded and rendered useless some of the open prairies of the western states. However, it is a great nectar-bearing flower for the production of honey and supports numerous pollinating insects, including migrating monarch butterflies in the north-central states such as Michigan.

LINK TO LEARNING

LINK TO LEARNING

Explore an interactive global database of exotic or invasive species.

Lakes and islands are particularly vulnerable to extinction threats from introduced species. In Lake Victoria, as mentioned earlier, the intentional introduction of the Nile perch was largely responsible for the extinction of about 200 species of endemic cichlids. The accidental introduction of the brown tree snake via aircraft (Figure 47.12) from the Solomon Islands to Guam in 1950 has 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. The brown tree snake is adept at exploiting human transportation as a means to migrate; one was even found on an aircraft arriving in Corpus Christi, Texas. Constant vigilance on the part of airport, military, and commercial aircraft personnel is required to prevent the snake from moving from Guam to other islands in the Pacific, especially Hawaii. 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.

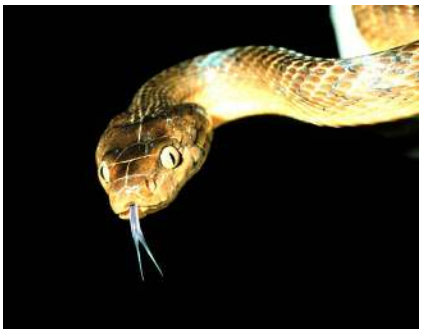


Figure 47.12 The brown tree snake, *Boiga irregularis*, is an exotic species that has caused numerous extinctions on the island of Guam since its accidental introduction in 1950. (credit: NPS)

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 47.13). 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 toad (*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 *Batrachochytrium dendrobatidis*, and can act as a reservoir for the disease. It also is a voracious predator in freshwater lakes.



Figure 47.13 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)

Early evidence suggests that another fungal pathogen, *Geomyces destructans*, introduced from Europe is responsible for white-nose syndrome, which infects cave-hibernating bats in eastern North America and has spread from a point of origin in western New York State (Figure 47.14). The disease has decimated bat populations and threatens extinction of species already listed as endangered: the Indiana bat, *Myotis sodalis*, and potentially the Virginia big-eared bat, *Corynorhinus townsendii virginianus*. How the fungus was introduced is unclear, but one logical presumption would be that recreational cavers unintentionally brought the fungus on clothes or equipment from Europe.



Figure 47.14 This little brown bat in Greeley Mine, Vermont, March 26, 2009, was found to have white-nose syndrome. (credit: Marvin Moriarty, USFWS)

CLIMATE CHANGE

Climate change, and specifically the *anthropogenic* (meaning, caused by humans) warming trend presently escalating, is recognized as a major extinction threat, particularly when combined with other threats such as habitat loss and the expansion of disease organisms. Scientists disagree about the likely magnitude of the effects, with extinction rate estimates ranging from 15 percent to 40 percent of species destined for extinction by 2050. Scientists do agree, however, that climate change will alter regional climates, including rainfall and snowfall patterns, making habitats less hospitable to the species living in them, in particular, the endemic species. 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. Previously, these two distinct species had separate ranges. Now, their ranges are overlapping and there are documented cases of these two species mating and producing viable offspring, which may or may not be viable crossing back to either parental species. Changing climates also throw off species' delicate timed adaptations to seasonal food resources and breeding times. Many contemporary mismatches to shifts in resource availability and timing have already been documented.



Figure 47.15 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 species of bears, which are capable of mating and producing viable offspring, are considered separate "ecological" species because 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 accelerating rate of warming in the arctic significantly reduces snowfall and the formation of sea ice. Without the ice, species like polar bears cannot successfully hunt seals, which are their only reliable source of food. Sea ice coverage has been decreasing since observations began in the mid-twentieth century, and the rate of decline observed in recent years is far greater than previously predicted.

Finally, global warming 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.

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8.5: PRESERVING BIODIVERSITY

LEARNING OBJECTIVES

By the end of this section, you will be able to do the following:

- Identify new technologies and methods for describing biodiversity
- Explain the legislative framework for conservation
- Describe principles and challenges of conservation preserve design
- Identify examples of the effects of habitat restoration
- Discuss the role of zoos in biodiversity conservation

Preserving biodiversity is an extraordinary challenge that must be met by greater understanding of biodiversity itself, changes in human behavior and beliefs, and various preservation strategies.

MEASURING BIODIVERSITY

The technology of molecular genetics and data processing and storage are maturing to the point where cataloguing the planet's species in an accessible way is now feasible. DNA barcoding is one molecular genetic method, which takes advantage of rapid evolution in a mitochondrial gene (cytochrome c oxidase 1) present in eukaryotes, except for plants, to identify species using the sequence of portions of the gene. However, plants may be 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 the 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 2017, close to 200,000 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, as already noted, at the present rate of description of new species, it will 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.

There is also the problem of understanding which species known to science are threatened and to what degree they are threatened. This task is carried out by the non-profit **IUCN** which, as previously mentioned, maintains the Red List—an online listing of endangered species categorized by taxonomy, type of threat, and other criteria (Figure 47.16). The Red List is supported by scientific research. In 2011, the list contained 61,000 species, all with supporting documentation.

VISUAL CONNECTION

VISUAL CONNECTION

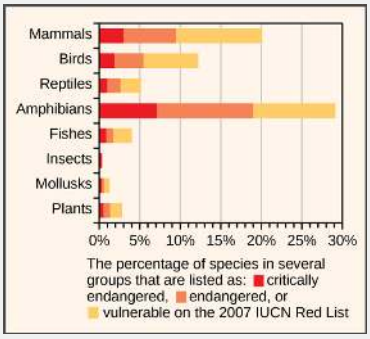


Figure 47.16 This chart shows the percentage of various animal species, by group, on the IUCN Red List as of 2007.

Which of the following statements is not supported by this graph?

1. There are more vulnerable fishes than critically endangered and endangered fishes combined.
2. There are more critically endangered amphibians than vulnerable, endangered and critically endangered reptiles combined.
3. Within each group, there are more critically endangered species than vulnerable species.
4. A greater percentage of bird species are critically endangered than mollusk species.

CHANGING HUMAN BEHAVIOR

Legislation throughout the world has been enacted to protect species. The legislation includes international treaties as well as national and state laws. 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 approximately 33,000 listed species from being transported across nations' 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 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 illegal trade in organisms and their parts is probably a market in the hundreds of millions of dollars. Illegal wildlife trade is monitored by another non-profit: Trade Records Analysis of Flora and Fauna in Commerce **(TRAFFIC)**.

Within many countries there are laws that protect endangered species and regulate hunting and fishing. In the United States, the **Endangered Species Act (ESA)** was enacted in 1973. Species at risk are listed by the Act; the U.S. Fish & Wildlife Service is required by law to develop plans that protect the listed species and bring them back to sustainable numbers. The Act, 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 it is listed. Additionally, species may be controversially taken off the list without necessarily having had a change in their situation. More fundamentally, the approach to protecting individual species rather than entire ecosystems is both inefficient and focuses efforts on a few highly visible and often charismatic species, perhaps at the expense of other species that go unprotected. At the same time, the Act has a critical habitat provision outlined in the recovery mechanism that may benefit species other than the one targeted for management.

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).

As already mentioned, the private non-profit sector plays a large role in the conservation effort both in North America and around the world. The approaches range from species-specific organizations to the broadly focused IUCN and TRAFFIC. The Nature Conservancy takes a novel approach. It purchases land and protects it in an attempt to set up preserves for ecosystems.

Although it is focused largely on reducing carbon and related emissions, the Paris Climate Agreement is a significant step toward altering human behavior in a way that should affect biodiversity. If the agreement is successful in its goal of halting global temperature rise, many species negatively affected by climate change may benefit. Assessments of the accord's implementation will not take place until 2023, and measurement of its effects will not be feasible for some time. However, the agreement, signed by over 194 countries, represents the world's most concerted and unified effort to reduce greenhouse gas emissions, embrace alternative energy sources, and ease climate pressure on ecosystems.

CONSERVATION IN PRESERVES

Establishment of wildlife and ecosystem 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. 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 to the preservation of biodiversity *and* the prevention of extinction.

HOW MUCH AREA TO PRESERVE?

Due to the way protected lands are allocated and the way biodiversity is distributed, it is challenging to determine how much land or marine habitat should be protected. The IUCN World Parks Congress estimated that 11.5 percent of Earth's land surface was covered by preserves of various kinds in 2003. We should note that this area is greater than previous goals; however, it only includes 9 out of 14 recognized major biomes. Similarly, individual animals or types of animals are not equally represented on preserves. For example, high quality preserves include only about 50 percent of threatened amphibian species. To guarantee that all threatened species will be properly protected, either the protected areas must increase in size, or the percentage of high quality preserves must increase, or preserves must be targeted with greater attention to biodiversity protection. Researchers indicate that more attention to the latter solution is required.

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.[5] 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 a 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 typically lower. Smaller islands are

also less geographically diverse so all things being equal, 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 able to colonize the island and find suitable niches on the island increases, 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 to support it. The critical size depends, in part, on the home range that is characteristic of the species. A preserve for wolves, which range 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 a 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 uses of the preserve for functions other than protection of species. These can include anything from timber extraction, mineral extraction, regulated hunting, human habitation, and nondestructive 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.

LIMITATIONS ON PRESERVES

Some of the limitations on preserves as conservation tools are evident from the discussion of preserve design. Political and economic pressures typically make preserves smaller, rather than 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 may 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 indicate that humans are growing more separate from nature, and that humans only operate in ways that do damage to biodiversity. Creating preserves may reduce the pressure on humans outside the preserve to be sustainable and non-damaging to biodiversity. On the other hand, properly managed, high quality preserves present opportunities for humans to witness nature in a less damaging way, and preserves may present some financial benefits to local economies. Ultimately, the economic and demographic pressures on biodiversity are unlikely to be mitigated by preserves alone. In order to fully benefit from biodiversity, humans will need to alter activities that damage it.

LINK TO LEARNING

LINK TO LEARNING

An interactive global data system of protected areas can be found at this website. Review data about individual protected areas by location or study statistics on protected areas by country or region.

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. The wolves (Figure 47.17) function to suppress elk and coyote populations and provide more abundant resources to the guild of carrion eaters. Reducing elk populations has allowed revegetation of riparian areas, which has increased the diversity of species in that habitat. Decreasing the coyote population has increased the populations of species that were previously suppressed by this predator. The number of species of

carrion eaters has increased because of the predatory activities of the wolves. In this habitat, the wolf is a keystone species, meaning a species that is instrumental in maintaining diversity in an ecosystem. Removing a keystone species from an ecological community may cause a collapse in diversity. The results from the Yellowstone experiment suggest that restoring a keystone species 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 those species; likewise, it also makes sense to attempt to return them to their ecosystem if they have been removed.

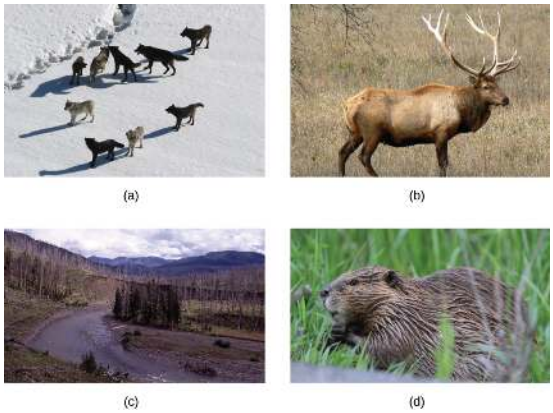


Figure 47.17 (a) The Gibbon wolf pack in Yellowstone National Park, March 1, 2007, represents a keystone species. The reintroduction of wolves into Yellowstone National Park in 1995 led to a change in the grazing behavior of (b) elk. To avoid predation, the elk no longer grazed exposed stream and riverbeds, such as (c) the Lamar Riverbed in Yellowstone. This allowed willow and cottonwood seedlings to grow and recolonized large areas. 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, which is a national movement that is accelerating in importance. 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 and because many dams no longer provide the benefit and functions that they did when they were first built. The measured benefits of dam removal include restoration of naturally fluctuating water levels (the purpose of dams is frequently to reduce variation in river flows), which leads to increased fish diversity and improved water quality. In the Pacific Northwest, dam removal projects are expected to increase populations of salmon, which is considered a keystone species because it transports key nutrients to inland ecosystems during its annual spawning migrations. In other regions such as the Atlantic coast, dam removal has allowed the return of 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 yet to occur or have happened too recently for the consequences to be measured. The large-scale ecological experiments that these removal projects constitute will provide valuable data for other dam projects slated either for removal or construction.

THE ROLE OF CAPTIVE BREEDING

Zoos have sought to play a role in conservation efforts both through captive breeding programs and education. The transformation of the missions of zoos from collection and exhibition facilities to organizations that are dedicated to conservation is ongoing and gaining strength. In general, it has been recognized that, except in some specific targeted cases, captive breeding programs for endangered species are inefficient and often prone to failure when the species are reintroduced to the wild. However, captive breeding programs have yielded some success stories, such as the California condor reintroduction to the Grand Canyon and the reestablishment of the Whooping Crane along the Midwest flyway.

Unfortunately, zoo facilities are far too limited to contemplate captive breeding programs for the numbers of species that are now at risk. Education is another potential positive impact of zoos on conservation efforts, particularly given the global trend to urbanization and the consequent reduction in contacts between people and wildlife. A number of studies have been performed to look at the effectiveness of zoos on people’s attitudes and actions regarding conservation; at present, the results tend to be mixed.

FOOTNOTES

- 5Robert H. MacArthur and Edward O. Wilson, E. O., *The Theory of Island Biogeography* (Princeton, N.J.: Princeton University Press, 1967).

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8.6: KEY TERMS

adaptive radiation
rapid branching through speciation of a phylogenetic tree into many closely related species

biodiversity
variety of a biological system, typically conceived as the number of species, but also applying to genes, biochemistry, and ecosystems

biodiversity hotspot
concept originated by Norman Myers to describe a geographical region with a large number of endemic species and a large percentage of degraded habitat

bush meat
wild-caught animal used as food (typically mammals, birds, and reptiles); usually referring to hunting in the tropics of sub-Saharan Africa, Asia, and the Americas

chemical diversity
variety of metabolic compounds in an ecosystem

chytridiomycosis
disease of amphibians caused by the fungus *Batrachochytrium dendrobatidis;* thought to be a major cause of the global amphibian decline

DNA barcoding
molecular genetic method for identifying a unique genetic sequence to associate with a species

ecosystem diversity
variety of ecosystems

endemic species
species native to one place

exotic species
(also, invasive species) species that has been introduced to an ecosystem in which it did not evolve

extinction
disappearance of a species from Earth; local extinction is the disappearance of a species from a region

extinction rate
number of species becoming extinct over time, sometimes defined as extinctions per million species–years to make numbers manageable (E/MSY)

genetic diversity
variety of genes in a species or other taxonomic group or ecosystem, the term can refer to allelic diversity or genome-wide diversity

heterogeneity
number of ecological niches

megafauna
large animals

secondary plant compound
compound produced as byproducts of plant metabolic processes that is usually toxic, but is sequestered by the plant to defend against herbivores

species-area relationship

relationship between area surveyed and number of species encountered; typically measured by incrementally increasing the area of a survey and determining the cumulative numbers of species

tragedy of the commons

economic principle that resources held in common will inevitably be overexploited

white-nose syndrome

disease of cave-hibernating bats in the eastern United States and Canada associated with the fungus *Geomyces destructans*

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8.7: CHAPTER SUMMARY

47.1 THE BIODIVERSITY CRISIS

Biodiversity exists at multiple levels of organization and is measured in different ways depending on the scientific goals of those taking the measurements. These measurements include numbers of species, genetic diversity, chemical diversity, and ecosystem diversity. The number of described species is estimated to be 1.5 million with about 17,000 new species being described each year. Estimates for the total number of species on Earth vary but are on the order of 10 million. Biodiversity is negatively correlated with latitude for most taxa, meaning that biodiversity is higher in the tropics. The mechanism for this pattern is not known with certainty, but several plausible hypotheses have been advanced.

Five mass extinctions with losses of more than 50 percent of extant species are observable in the fossil record. Biodiversity recovery times after mass extinctions vary, but may be as long as 30 million years. Recent extinctions are recorded in written history and are the basis for one method of estimating contemporary extinction rates. The other method uses measures of habitat loss and species-area relationships. Estimates of contemporary extinction rates vary, but some rates are as high as 500 times the background rate, as determined from the fossil record, and are predicted to rise.

47.2 THE IMPORTANCE OF BIODIVERSITY TO HUMAN LIFE

Humans use many compounds that were first discovered or derived from living organisms as medicines: secondary plant compounds, animal toxins, and antibiotics produced by bacteria and fungi. More medicines will undoubtedly be discovered in nature. Loss of biodiversity will impact the number of pharmaceuticals available to humans.

Crop diversity is a requirement for food security, and it is being lost. The loss of wild relatives to crops also threatens breeders' abilities to create new varieties. Ecosystems provide ecosystem services that support human agriculture: pollination, nutrient cycling, pest control, and soil development and maintenance. Loss of biodiversity threatens these ecosystem services and risks making food production more expensive or impossible. Wild food sources are mainly aquatic, but few of these resources are being managed for sustainability. Fisheries' ability to provide protein to human populations is threatened when extinction occurs.

Biodiversity may provide important psychological benefits to humans. Additionally, there are moral arguments for the maintenance of biodiversity.

47.3 THREATS TO BIODIVERSITY

The core threats to biodiversity are human population growth and unsustainable resource use. To date, the most significant causes of extinctions are habitat loss, introduction of exotic species, and overharvesting. Climate change is predicted to be a significant cause of extinctions in the coming century. Habitat loss occurs through deforestation, damming of rivers, and other disruptive human activities. Overharvesting is a threat particularly to aquatic species, while the taking of bush meat in the humid tropics threatens many species in Asia, Africa, and the Americas. Exotic species have been the cause of a number of extinctions and are especially damaging to islands and lakes. Exotic species' introductions are increasing damaging native ecosystems around the world because of the increased mobility of human populations and growing global trade and transportation. Climate change is forcing range changes that may lead to extinction. It is also affecting adaptations to the timing of resource availability that negatively affects species in seasonal environments. The impacts of climate change are greatest in the arctic. Global warming will also raise sea levels, eliminating some islands and reducing the area of all others.

47.4 PRESERVING BIODIVERSITY

New technological methods such as DNA barcoding and information processing and accessibility are facilitating the cataloging of the planet's biodiversity. There is also a legislative framework for biodiversity protection. International treaties such as CITES regulate the transportation of endangered species across international borders. Legislation within individual countries protecting species and agreements on global warming have had limited success; the Paris Climate accord is currently being implemented as a means to reduce global climate change.

In the United States, the Endangered Species Act protects listed species but is hampered by procedural difficulties and a focus on individual species. The Migratory Bird Act is an agreement between Canada and the United States to protect migratory birds. The non-profit sector is also very active in conservation efforts in a variety of ways.

Conservation preserves are a major tool in biodiversity protection. Presently, 11 percent of Earth's land surface is protected in some way. The science of island biogeography has informed the optimal design of preserves; however, preserves have limitations imposed by political and economic forces. In addition, climate change will limit the effectiveness of preserves in the future. A downside of preserves is that they may lessen the pressure on human societies to function more sustainably outside the preserves.

Habitat restoration has the potential to restore ecosystems to previous biodiversity levels before species become extinct. Examples of restoration include reintroduction of keystone species and removal of dams on rivers. Zoos have attempted to take a more active role in conservation and can have a limited role in captive breeding programs. Zoos also have a useful role in education.

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8.8: VISUAL CONNECTION QUESTIONS

1.

Figure 47.6 Scientists measured the relative abundance of fern spores above and below the K-Pg boundary in this rock sample. Which of the following statements most likely represents their findings?

1. An abundance of fern spores from several species was found below the K-Pg boundary, but none was found above.
2. An abundance of fern spores from several species was found above the K-Pg boundary, but none was found below.
3. An abundance of fern spores was found both above and below the K-Pg boundary, but only one species was found below the boundary , and many species were found above the boundary.
4. Many species of fern spores were found both above and below the boundary, but the total number of spores was greater below the boundary.

2.

Figure 47.9 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?

3.

Converting a prairie to a farm field is an example of _____.

1. overharvesting
2. habitat loss
3. exotic species
4. climate change

4.

Figure 47.16 Which of the following statements is not supported by this graph?

1. There are more vulnerable fishes than critically endangered and endangered fishes combined.
2. There are more critically endangered amphibians than vulnerable, endangered and critically endangered reptiles combined.
3. Within each group, there are more critically endangered species than vulnerable species.
4. A greater percentage of bird species are critically endangered than mollusk species.

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8.9: REVIEW QUESTIONS

5.

With an extinction rate of 100 E/MSY and an estimated 10 million species, how many extinctions are expected to occur in a century?

1. 100
2. 10,000
3. 100,000
4. 1,000,000

6.

An adaptive radiation is_____.

1. a burst of speciation
2. a healthy level of UV radiation
3. a hypothesized cause of a mass extinction
4. evidence of an asteroid impact

7.

The number of currently described species on the planet is about _____.

1. 17,000
2. 150,000
3. 1.5 million
4. 10 million

8.

A mass extinction is defined as _____.

1. a loss of 95 percent of species
2. an asteroid impact
3. a boundary between geological periods
4. a loss of 50 percent of species

9.

A secondary plant compound might be used for which of the following?

1. a new crop variety
2. a new drug
3. a soil nutrient
4. a pest of a crop pest

10.

Pollination is an example of _____.

1. a possible source of new drugs
2. chemical diversity
3. an ecosystem service
4. crop pest control

11.

What is an ecosystem service that performs the same function as a pesticide?

1. pollination
2. secondary plant compounds
3. crop diversity
4. predators of pests

12.

Which two extinction risks may be a direct result of the pet trade?

1. climate change and exotic species introduction
2. habitat loss and overharvesting

3. overharvesting and exotic species introduction
4. habitat loss and climate change

13.

Exotic species are especially threatening to what kind of ecosystem?

1. deserts
2. marine ecosystems
3. islands
4. tropical forests

14.

Certain parrot species cannot be brought to the United States to be sold as pets. What is the name of the legislation that makes this illegal?

1. Red List
2. Migratory Bird Act
3. CITES
4. Endangered Species Act (ESA)

15.

What was the name of the first international agreement on climate change?

1. Red List
2. Montreal Protocol
3. International Union for the Conservation of Nature (IUCN)
4. Kyoto Protocol

16.

About what percentage of land on the planet is set aside as a preserve of some type?

1. 1 percent
2. 6 percent
3. 11 percent
4. 15 percent

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8.10: CRITICAL THINKING QUESTIONS

17.

Describe the evidence for the cause of the Cretaceous–Paleogene (K–Pg) mass extinction.

18.

Describe the two methods used to calculate contemporary extinction rates.

19.

Explain how biodiversity loss can impact crop diversity.

20.

Describe two types of compounds from living things that are used as medications.

21.

Describe the mechanisms by which human population growth and resource use causes increased extinction rates.

22.

Explain what extinction threats a frog living on a mountainside in Costa Rica might face.

23.

Describe two considerations in conservation preserve design.

24.

Describe what happens to an ecosystem when a keystone species is removed.

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