

BIS 2B: INTRODUCTION TO BIOLOGY - ECOLOGY & EVOLUTION



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CHAPTER OVERVIEW

1: Introduction to Biology

Biology is the study of living organisms, including their physical structure (from cells to whole individuals), chemical processes (such as metabolism), physiology, and development. This is a very broad definition because the scope of biology is vast. Biologists may study anything from the microscopic view of a cell to ecosystems and the whole living planet. Listening to the daily news, you will quickly realize how many aspects of biology are discussed every day. For example, recent news topics include *Escherichia coli* 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.

What does the study of biology share with other scientific disciplines? Science (from the Latin *scientia*, meaning “knowledge”) can be defined 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 the application of the 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.

[1.1: The Scientific Method](#)

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1.1: The Scientific Method

Biologists, and other scientists, study the world using a formal process referred to as **the scientific method**. The scientific method was first documented by Sir Francis Bacon (1561–1626) of England, and can be applied to almost all fields of study. The scientific method is founded upon observation, which then leads to a question and the development of a hypothesis which answers that question. The scientist can then design an experiment to test the proposed hypothesis, and makes a prediction for the outcome of the experiment, if the proposed hypothesis is true. In the following sections, we will use a simple example of the scientific method, based on a simple observation of the classroom being too warm.

Proposing a Hypothesis

A hypothesis is one possible answer to the question that arises from observations. In our example, the observation is that the classroom is too warm, and the question that arises from that observation is *why* the classroom is too warm. One (of many) hypotheses is “The classroom is warm because no one turned on the air conditioning.” Another hypothesis could be “The classroom is warm because the heating is set too high.”

Once a hypothesis has been developed, the scientist then makes a prediction, which is similar to a hypothesis, but generally follows the format of “If . . . then” In our example, a prediction arising from the first hypothesis might be, “*If* the air-conditioning is turned on, *then* the classroom will no longer be too warm.” The initial steps of the scientific method (observation to prediction) are outlined in Figure 1.1.1.

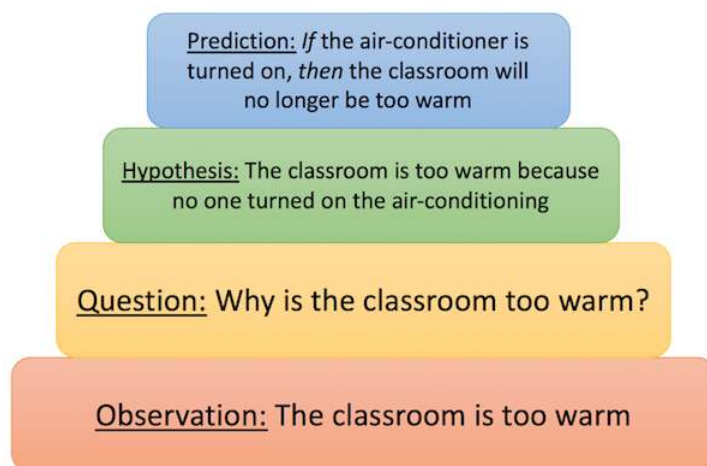


Figure by L Gerhart-Barley

Testing a Hypothesis

A valid hypothesis must be testable. It should also be falsifiable, meaning that it can be disproven by experimental results. Importantly, science does not claim to “prove” anything because scientific understandings are always subject to modification with further information. 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 tests the hypothesis. Therefore, if the results of the experimental group 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, then the hypothesis that the air conditioning was not turned on should be rejected. To test the second hypothesis, the student could check the settings of the classroom heating unit. If the heating unit is set at an appropriate temperature, then this hypothesis should also be rejected. Each hypothesis should be tested by carrying out appropriate experiments. Be aware that rejecting one hypothesis does not determine whether or not the other hypotheses can be accepted; it simply eliminates one hypothesis that is not valid. Using the scientific method, the hypotheses that are inconsistent with experimental data are rejected.

While this “warm classroom” example is based on observational results, other hypotheses and experiments might have clearer controls. For instance, a student might attend class on Monday and realize they 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.

Exercise 1.1.1

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

1. Observation
 2. Question
 3. Hypothesis (answer)
 4. Prediction
 5. Experiment
 6. Result
- a. The car battery is dead.
 - b. If the battery is dead, then the headlights also will not turn on.
 - c. My car won't start.
 - d. I turn on the headlights.
 - e. The headlights work.
 - f. Why does the car not start?

Answer

C, F, A, B, D, E

The scientific method may seem overly rigid and structured; however, there is flexibility. Often, the process of science is not as linear as the scientific method suggests and experimental results frequently inspire a new approach, highlight patterns or themes in the study system, or generate entirely new and different observations and questions. In our warm classroom example, testing the air conditioning hypothesis could, for example, unearth evidence of faulty wiring in the classroom. This observation could then inspire additional questions related to other classroom electrical concerns such as inconsistent wireless internet access, faulty audio/visual equipment functioning, non-functional power outlets, flickering lighting, etc. Notice, too, that the scientific method can be applied to solving problems that aren't necessarily scientific in nature.

Credits

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1.2: What is Ecology?

Ecology is the study of how organisms interact with each other and with the physical environment in which they live. It is a large field of study and incorporates research at many spatial and temporal scales. Examples of ecological research include impacts of climatic change on species range distributions, patterns of infectious disease outbreaks, the effect of nutrient availability on ecosystem function, etc. In his 1911 book *My First Summer in the Sierra*, John Muir famously wrote ‘when we try to pick out anything by itself, we find it hitched to everything else in the Universe.’ This quote sums up the unifying tenet of ecology – that all biotic and abiotic factors are linked to interact with one another, and that a change in one factor will likely cause a change in all of the factors to which is linked.

Levels of Ecological Study

Ecology incorporates research at many spatial scales, from a single individual to the entire biosphere. The major levels of ecological study are illustrated in Fig 1.2.1. In some cases, research studies and systems span multiple levels; however, each scale has particular questions and approaches that are commonly used. To illustrate ecological research at each scale, we will consider the research projects of researchers in the [lab of Dr. Brian Todd](#) in the [Wildlife, Fish, and Conservation Biology Department](#) at UC Davis.



Figure 1.2.1: Examples of scale in ecological research. UC Davis Arboretum photos by L Gerhart-Barley, Earth image from Wikimedia Commons¹.

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 example, researchers in the Todd Lab are interested in the salt tolerance of different turtle species such as the Western Pond Turtle (*Emys marmorata*) shown in Figure 1.2.1, which is native to California. Salt tolerance determines the waterways in which the Western Pond Turtles can survive and therefore contributes to the species range and distribution.

A **population** is a group of interbreeding organisms that are members of the same species living in the same area at the same time. The population may have natural or artificial boundaries: natural boundaries might be rivers, mountains, or deserts, while examples of artificial boundaries include mowed grass, manmade structures, or roads. The study of population ecology focuses on the number of individuals in an area and how and why population size changes through time. The Todd Lab studies several populations of turtles, including the population residing in the [UC Davis Arboretum and Public Garden](#) waterway. The Western Pond Turtle is federally listed as vulnerable and is a [California Species of Special Concern](#) (our state-level conservation listing), so campus researchers and the Arboretum waterway managers are concerned about the size of the population of Western Pond Turtles in the waterway, particularly if the population is declining. The Todd Lab regularly traps turtles in the Arboretum and documents the size and sex of each turtle found. Small turtles, like the one shown in Fig 1.2.2a, indicate that the Arboretum population is successfully producing new offspring. In addition, Todd’s team marks each Western Pond Turtle with unique shell notches, which allow the researchers to identify how often they catch the same turtle and to track individuals throughout their lives. Figure 1.2.2b shows markings on a turtle captured in April 2019.

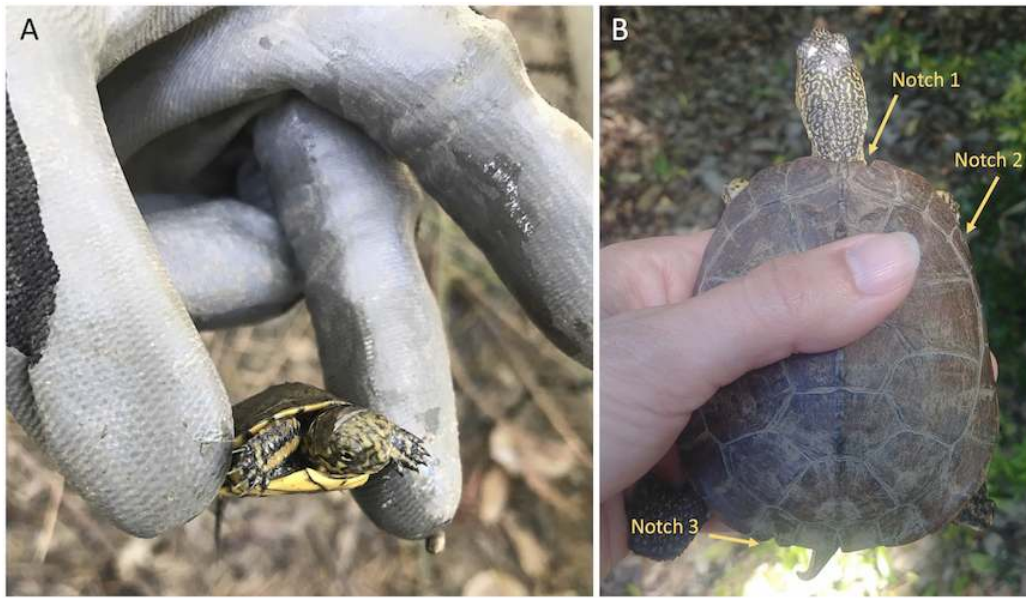


Figure 1.2.2: Juvenile Western Pond Turtles documented in the UC Davis Arboretum Waterway April 2019. Notches in B are identification markers applied by researchers for tracking individual turtles throughout their lifetime (Photo A by N. Suzuki, Photo B by L. Gerhart-Barley)

A biological **community** consists of populations of different species living in the same area at the same time. Community ecologists are interested in the interactions within and among these species and the processes driving these interactions. Questions about interactions within a single species often focus on competition among members of the same species for a limited resource. Ecologists also study interactions between various species. These 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. The Western Pond Turtle is not the only turtle species that lives in the Arboretum waterway; several other species have been introduced to the waterway, probably through the release of pet turtles no longer wanted by their owners. The most common turtle species is the Red-Eared Slider (*Trachemys scripta elegans*), though several other species such as soft-shelled turtles, snapping turtles, and map turtles have also been identified in the waterway (Fig 1.2.3). There are, of course, many other non-turtle species that live in the waterway as well, including European carp, mallards and wood ducks, and possibly even river otters, not to mention a variety of aquatic plants and algae, and a plethora of insects. The potential interactions between these species and the Western Pond Turtles might be important drivers of their population sizes. In particular, previous research by former UC Davis professor [Dr. Brad Shaffer](#) looked at competition between the Western Pond Turtle and the introduced Red-Eared Slider for basking sites within the Arboretum waterway ([Lambert et al 2013](#)).



Figure 1.2.3: A Western Pond Turtle (center, note the lack of red and yellow stripes on the head) basks on a log in the Arboretum waterway with five Red-Eared Sliders and a Mallard chick in May 2018. Photo by L. Gerhart-Barley

Ecosystem ecology is an extension of organismal, population, and community ecology. The ecosystem is composed of all the biotic components (living organisms) in an area along with the abiotic components (non-living factors) of that area. Some of the abiotic components include air, water, and soil. Ecosystem biologists ask questions about how nutrients and energy move among organisms and how environmental factors such as temperature, precipitation, salinity, etc affect species in the habitat and interactions between species. The Arboretum waterway managers are particularly interested in how the built environment around the waterway (paths, trails, concrete retainers, etc) might affect the Western Pond Turtle. Some parts of the waterway have soil banks covered in native vegetation, while others have bare ground, and still others have concrete retaining walls (Fig 1.2.4). Previous research by Dr. Shaffer and his team determined that Western Pond Turtles are more commonly found basking on concrete structures in shallower water in areas less disturbed by human activities ([Lambert et al 2013](#)).

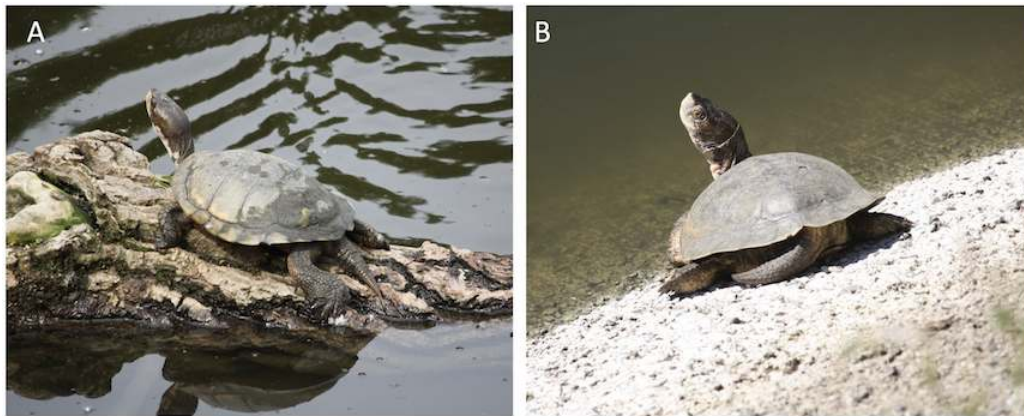


Figure 1.2.4: Western Pond Turtles using natural (A) and human-built (B) basking sites. Photos by L Gerhart-Barley

Landscape ecology deals with questions of connectivity between ecosystems, including movement of organisms and compounds between ecosystems and the effects of boundaries or edges where different ecosystems come into contact (Fig 1.2.5). A landscape ecologist might study habitat fragmentation (such as deforestation) or the migration of organisms between ecosystems, etc. The Arboretum waterway ecosystem is part of a broader landscape of aquatic and terrestrial ecosystems, including upstream and downstream Putah Creek, grassy lawns, shrublands, forests, and the urban ecosystems of the UC Davis campus and surrounding city of Davis. This landscape could influence migration of the Western Pond Turtle (and other Arboretum inhabitants) to other nearby waterways and could directly affect the Arboretum waterway ecosystem by influencing factors such as water quality (ie. clarity), temperature, sunlight availability, nutrient availability, disturbance (especially by humans), etc.



Figure 1.2.5: An example of a landscape of connecting ecosystems in the Arboretum. At Spafford Lake, the Arboretum waterway lies between grassy lawns on the western bank (foreground) and forested gardens on the eastern bank (background). Photo by L Gerhart-Barley

At its broadest, ecology considers the entire **biosphere**, all habitats on earth in which living organisms exist. Global ecological questions include the impacts of atmospheric and oceanic currents, the role of greenhouse gases concentrations in the global energy budget, the effects of climate change on ecosystems and organisms, etc

In this section, we have focused on categorizing ecology by its spatial scale, though many other types of categorization are possible. For example, **disease ecology** focuses on the evolution, virulence, and transmission of infectious pathogens or parasites, and **human ecology** focuses on human interactions with the environment including societal, cultural, technological, and institutional relationships. These ‘other’ ecologies can operate at any of the scales described above. For instance, disease ecology might focus on the organismal level (physiological impacts of disease on individuals), the population level (transmission of disease between individuals of the same species), or community level (transmission of disease across species), etc.

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1.3: What is Evolution?

At its simplest, **evolution** is any change in heritable traits in a population of organisms across generations. These changes may be the result of natural selection, genetic drift, mutation, etc – processes that we will consider in depth later in the course. All populations experience evolutionary change, as influenced by their environment, their interactions with other organisms, and random chance. Like ecology, we can consider evolution at different scales.

Microevolution is genetic change that occurs over small timescales and results in small changes in heritable traits. For example, Drs. Peter and Rosemary Grant studied medium ground finches (*Geospiza fortis*, Fig 1.3.1) in the Galápagos Islands for over 40 years, tracking the body size, beak size, weight, and other traits in the entire population over numerous generations. In 1977 a major drought hit the island of Daphne Major where the Grants were performing their study. The drought caused a change in the vegetation of the island, whose seeds are the food source for the ground finches. In the generation following the drought, the Grants documented an increase in the beak size of the ground finches in response to the change in seeds on which they feed. This relatively small change in a heritable trait across generations represents a microevolutionary response to the 1977 drought.



Figure 1.3.1: A medium ground finch, *Geospiza fortis*. Image from Wikimedia Commons¹.

Macroevolution is genetic change that occurs over long time scales, resulting in large changes in heritable traits in a population; changes large enough that we consider this population a unique taxonomic group, or species. Macroevolution is sometimes also termed **speciation** (the process by which a new species arises). This is the scale of evolutionary change that most people think of when someone mentions ‘evolution’. For example, the medium ground finch is not the only finch species in the Galápagos Islands. The genus *Geospiza* contains nine species, all of which are found exclusively in the Galápagos Islands. Approximately 2 million years ago, the ancestor of these species migrated to the Galápagos Islands from South America. Between then and now, the birds migrated throughout the Galápagos Islands and across generations experienced different microevolutionary changes. Eventually, these small differences accumulated to the point that individuals of different populations are genetically distinct, no longer interbreed with one another, and perform different ecological roles in the habitat (for instance, some feed on seeds, while others feed on insects). Consequently, we now consider them different species. *Geospiza* is not the only group of finches on the Galápagos Islands - Figure 1.3.2 illustrates differences in head and beak shape between several finch groups on the Islands.



Figure 1.3.2: Beak and head shape of two *Geospiza* finches and two other Galápagos finch species. Clockwise from top left: *Geospiza magnirostris*, *Geospiza fortis*, *Certhidea olivacea*, *Camarhynchus parvulus*. Image from Wikimedia Commons².

It is important to note that microevolution and macroevolution are not different processes. Both relate to genetic changes in a population across generations; the only difference is the timescale on which the two operate. Macroevolution is the accumulation of microevolutionary changes over a long period of time to the point that the population is unique from other populations, and is considered a distinct species.

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1.4: Linking Ecology and Evolution

Why do we study evolution and ecology together in this course?

In 1973, evolutionary biologist Theodosius Dobzhansky wrote a now-famous essay titled *Nothing in Biology Makes Sense Except in the Light of Evolution*. In this essay, Dobzhansky argued that evolution is the underlying unifying theme for all of biological study and that understanding life on earth necessarily requires considering evolutionary processes and impacts. The title of this essay became a famous quote highlighting the foundational importance of evolution to all biological concepts and processes and is often repeated by evolutionary biologists.

In 2008, Drs. Peter and Rosemary Grant wrote a scientific text on their decades-long work studying the Galápagos finches titled *How and Why Species Multiply: The Radiation of Darwin's Finches*. In this book, they discussed Dobzhansky's famous quote and argued for a slight adjustment. The Grants argued that "nothing in evolutionary biology makes sense except in the light of ecology."

The following year, Dr. Fanie Pelletier and her colleagues published a paper on the links between evolutionary and ecological processes and also argued for an adjustment to Dobzhansky's quote. These authors stated that "nothing in evolution or ecology makes sense except in the light of the other."

These three quotes illustrate why evolution and ecology are grouped together in this course. As you will see throughout the quarter, ecological interactions frequently drive evolutionary change. For example, predation drives the development of defenses in prey such as camouflage, armor, or toxins. As you will also see, natural selection relies on interactions between a population and other organisms or the environment and so is an ecological interaction as well as an evolutionary process. In these ways, and others, ecological interactions and evolutionary trajectories are inextricably linked and therefore important to study together.



Figure 1.4.1: From left, Theodosius Dobzhansky, Rosemary and Peter Grant, Fanie Pelletier. Images of Dobzhansky¹ and Grants² from Wikimedia Commons, Image of Pelletier from Université de Sherbrooke³.

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3. <https://www.usherbrooke.ca/biologie/personnel/professeurs/ecologie-terrestre/fanie-pelletier/>

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CHAPTER OVERVIEW

2: Biodiversity

Biodiversity is a broad term that encompasses any type of variation that exists in biological systems (Figure 2.1). Though we most commonly discuss biological diversity as variation in the species that occupy the same habitat at the same time, variation exists at all levels of biological organization. A genus that contains many species would have higher diversity than a genus that contains only a few species. The same is true for a family that includes many genera, an order that includes many families, a class that includes many orders, a phylum that includes that many classes, and a kingdom that includes many phyla. Similarly, a species that exhibits a variety of genotypes would be said to have higher **genetic diversity** than a species with limited variation in genotypes. Also, a single genotype that exhibits a variety of phenotypes (termed **plasticity**) would have higher diversity than a genotype that results in only a single phenotype.

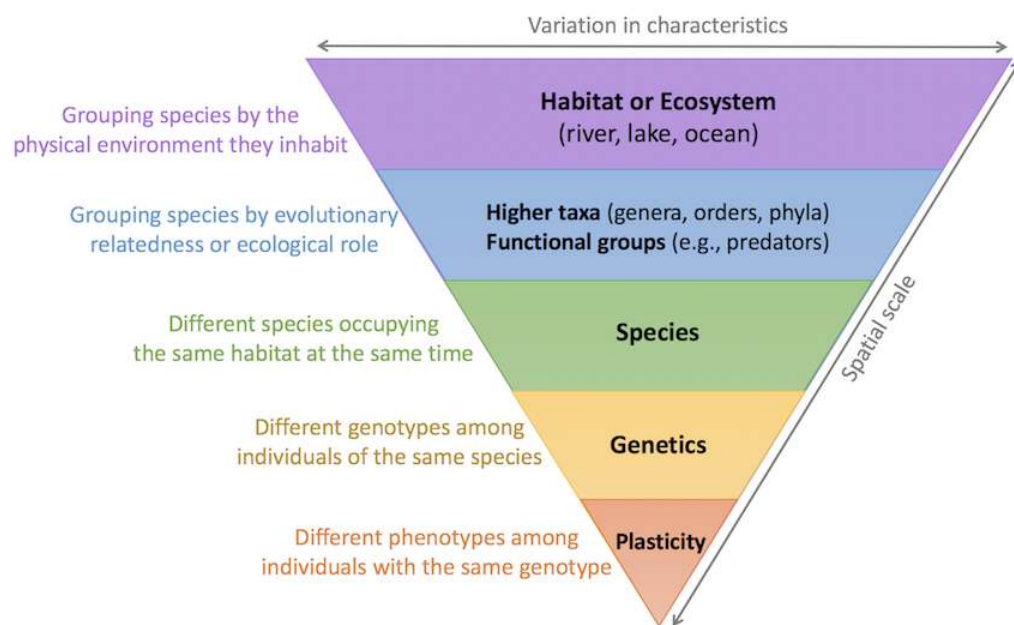


Figure 2.1: Schematic of the magnitude and type of diversity exhibited at different scales.
This section focuses on species diversity. Figure by L Gerhart-Barley

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- 2.1: Species Concepts
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2.1: Species Concepts

Quantifying species diversity requires developing a definition of a species. We would not expect all members of a species to be identical, so we must consider what magnitude and types of differences between individuals would lead us to consider them members of different species. A **species concept** is, therefore, a working definition of a species and/or a methodology for determining whether or not two organisms are members of the same species. In this section, we will consider three species concepts that are commonly used by scientists. All species concepts have limitations and work better for some organismal groups than others. Each section below considers the definition of the species concept, its assumptions and limitations, and examples of groups for which that species concept does, and does not, easily apply.

The Biological Species Concept

By far the most well-known species concept is the biological species concept, which was proposed by evolutionary biologist Ernst Mayr. The **biological species concept** states that a species is a group of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups. **Reproductive isolation** can occur in several ways (which we will discuss in detail later in the quarter); individuals of different groups may not mate with each other, their mating may not produce offspring, or the offspring produced may not be viable (able to survive) or fertile (able to reproduce).

In some cases, the biological species concept is straightforward and easy to apply. For instance, the western meadowlark (*Sturnella neglecta*) and the eastern meadowlark (*Sturnella magna*), both shown in Figure 1, respectively inhabit the western and eastern halves of North America. Despite the fact that their breeding ranges overlap throughout many upper midwestern states, including Michigan, Wisconsin, Illinois, Iowa, Missouri and Minnesota, the two groups do not interbreed. The courtship songs of the males of each species are distinctly different and females of each species respond to the songs of the males of their own species, leading to strong reproductive isolation between the two groups despite a high degree of similarity in appearance.



Figure 2.1.1: Males of the western meadowlark, *Sturnella neglecta* (left) and the eastern meadowlark *Sturnella magna* (right).
Images from Wikimedia Commons^{1,2}

In many cases, however, the biological species concept is difficult or impossible to use. For example, the definition's focus on interbreeding means this concept cannot be applied to asexual organisms, such as bacteria. Additionally, it can only be applied to groups for which detailed reproductive data are available, or at least obtainable. It is therefore impossible to apply the biological species concept to long-extinct species for which reproductive data do not exist and can no longer be obtained. It can also be difficult to apply the biological species concept to groups for which little is known about their reproductive biology or behavior. In these cases, extensive research would be required to determine the degree to which individuals do or do not interbreed with other groups before being able to clearly identify species boundaries. Additionally, some groups have complex patterns of reproductive connectivity and isolation, such as the *Ensatina* salamander group shown in Fig 2. Systems like *Ensatina* are termed 'ring species'

because they form a ring around a particular geographic barrier, in this case, California's Central Valley. As the group spread around the valley, populations maintained reproductive connectivity (ie. interbreeding) with nearby populations, but developed reproductive isolation from geographically distant populations. In the diagram below, interbreeding is shown as a gradation in color between two populations and reproductive isolation is shown as a solid line. For example, *E. oregonensis* (in red) can interbreed with *E. picta* (orange), *E. xanthoptica* (yellow), and *E. platensis* (pink), but none of the other species. Similarly, *E. xanthoptica* (yellow) can interbreed with *E. eschscholtzii* (green) and *E. oregonensis* (red), but none of the other species. In this case, the biological species concept leads to nonsensical and contradictory conclusions: *E. oregonensis*, *E. xanthoptica*, and *E. eschscholtzii* are members of the same species, but *E. oregonensis* and *E. eschscholtzii* are different species.

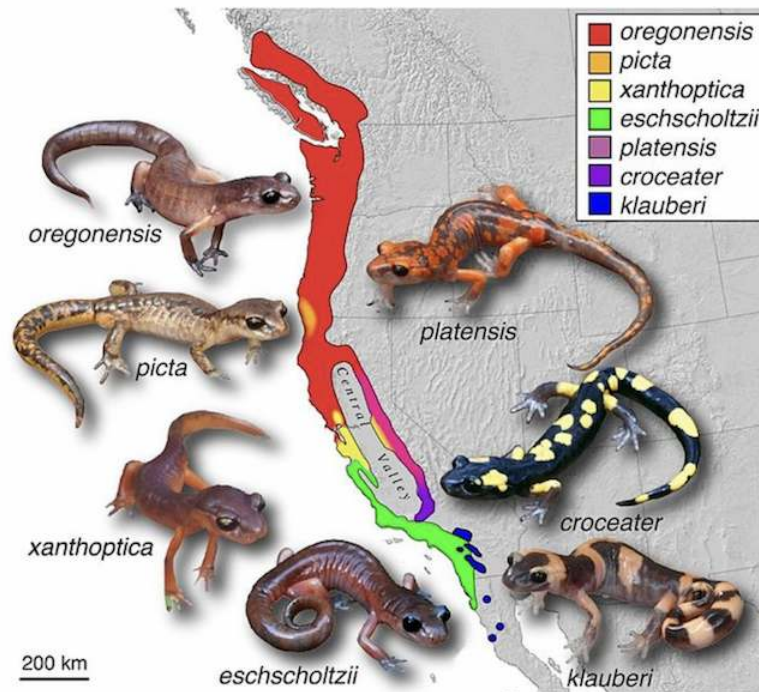


Figure 2.1.2: Range map for Ensatina species on the western coast of North America. Gradations in color (ex: *E. oregonensis* and *E. picta*) denote interbreeding between the two species, while solid lines (ex: *E. klauberi* and *E. eschscholtzii*) denote reproductive isolation. Image from Wikimedia Commons³.

More philosophically, the biological species concept also considers species at only a single point in time (the present) and ignores the evolutionary and ecological processes that shaped reproductive isolation between groups.

The Lineage Species Concept

Due to the limitations of the biological species concept described above, other species concepts have been developed. The **lineage species concept** defines species as groups of organisms that share a pattern of ancestry and descent and which form a single branch on the tree of life (Fig 3). This concept focuses more on the evolutionary history that has shaped the species as we see it today, and increasingly relies on genetic data to assign individuals to species. The lineage species concept resolves some of the problems of the biological species concept since it can be applied to asexual species and those for which detailed reproductive behavioral data are unavailable. It's reliance on genetic data makes it also difficult to apply to long-extinct species; however, recent advances in genetic analysis have allowed scientists to extract DNA from recently extinct organisms such as Neanderthals and woolly mammoths. Scientists using the lineage species concept must still consider what type and magnitude of genetic differences, and in what portions of the genome, constitute different species and must employ modern computational tools to manage the increasingly large datasets produced in genetic analyses.

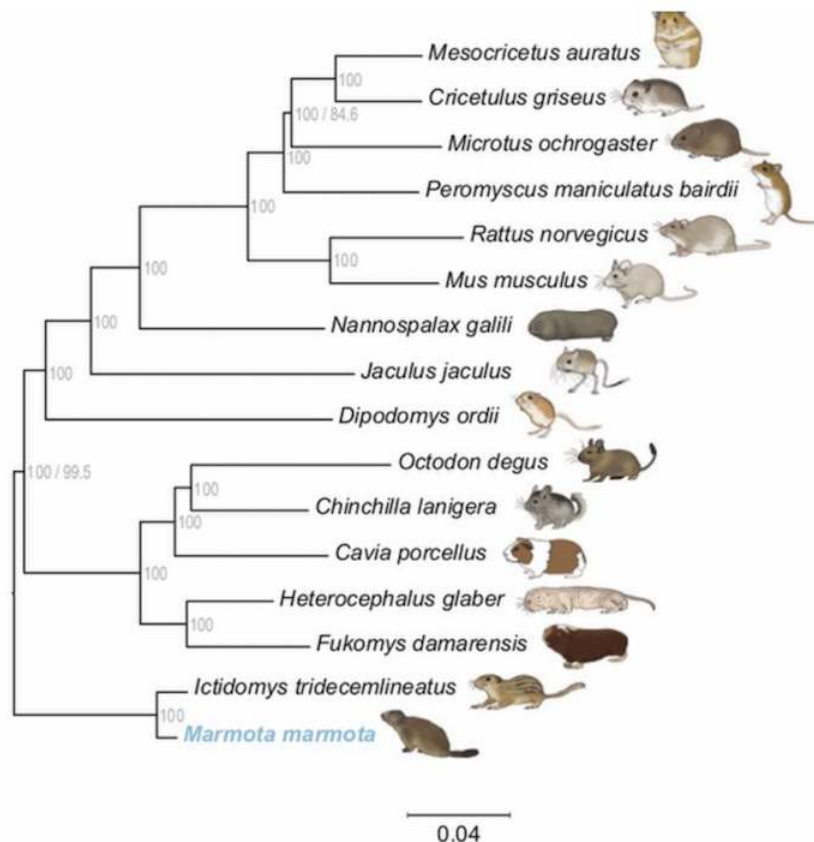


Figure 2.1.3: A phylogenetic tree of the order Rodentia (rodents), representing the lineage species concept's focus on species being identified as unique branches on a phylogenetic tree. Image from Wikimedia Commons⁴

The Morphological Species Concept

How do scientists define species in groups where there is limited or unavailable data on reproductive behavior or genetic similarity? Consider, for example, the two trilobites shown in Figure 2.1.4. Both of the fossils shown in the figure are members of the Order Phacopidae, which went extinct during the end-Devonian mass extinction event that occurred approximately 360 million years ago. Consequently, the only evidence that remains of their existence is fossils; there is no behavioral data on reproductive isolation or connectivity with other trilobites and the fossils are old enough that their DNA has degraded beyond our current analytical capabilities. How then, do we define species in trilobites? The **morphological species concept** is frequently applied in such cases, as it relies entirely on morphology (the physical structures or traits of an organism).

As you look at two photos in Fig 4, you will notice clear morphological differences. The fossil on the right has large spines jutting from both its head and rear ends (in trilobites, these are termed the cephalon and pygidium, respectively). Additionally, the spines along the side of the trilobite's thorax are much larger and more pronounced in the fossil on the right. These morphological differences lead us to categorize these fossils as members of different species. In this case, the differences are large enough that we even categorize these fossils as members of different genera and families.



Figure 2.1.4: Two trilobites in the order Phacopidae; *Hollardops mesocristata* (left) and *Cheirurus ingricus* (right). Images from Wikimedia Commons^{5,6}.

Since all organisms have physical traits, the morphological species can be used on any group of organisms on Earth. The major limitation to this species concept, however, is that morphology can be very misleading. Consider, for example, the shark and dolphin shown in Figure 5. These organisms have many morphological similarities in their body shape and coloration; however, we know from genetic analyses and more detailed morphological studies (on internal structures, etc) that sharks are more closely related to rays and other fish and dolphins are more closely related to whales and other mammals. The similarities that we first notice in these organisms are due to the similarities in the marine environment in which both organisms live and not to relatedness between the organisms. Consequently, the morphological species concept is often only used when other species concepts cannot be applied (for example, in the trilobite case) or in conjunction with other species concepts described above.



Figure 2.1.5: a bullshark (*Carcharhinus leucas*, left) and a bottlenose dolphin (*Tursiops truncatus*, right). Images from Wikimedia Commons^{7,8}.

Linking Species Concepts

Most scientists generally agree that a species is a group of organisms that share an evolutionary and ecological history and that are distinct from other groups. The primary difference in the species concepts described above is the forms of evidence used to quantify those differences and to categorize individuals as members of a particular species. The biological species concept relies on behavioral data and emphasizes reproductive isolation between groups. The lineage species concept relies on genetic data and emphasizes distinct evolutionary trajectories between groups, which result in distinct lineages (branches on a phylogenetic tree). The morphological species concept relies on morphological data and emphasizes groups of physical traits that are unique to each species. These lines of evidence are not mutually exclusive and so multiple species concepts may be used together to define species boundaries. Regardless of the species concept used, not all organisms are easily categorized into distinct groups and so conversations around species concepts, species boundaries, and the evidence used to define them are a dynamic field of evolutionary biology. You will practice defining group boundaries in Lab 1: Discovering Diversity. In this lab, you will categorize organisms into 'operational taxonomic units' (OTUs) using the morphological species concept.

Naming Species

Carl Linnaeus began formally naming and categorizing species in 1735 in his publication *Systema Naturae*. Linnaeus developed the **binomial nomenclature** system for naming species, which is still used by scientists today. In this system, each species is given a two-word (binomial) Latin name. The first word is the generic name, which is shared among all the species in that genus. The second word is the specific epithet and is unique among species in that genus. For instance, all juniper trees have the genus name *Juniperus* and each species has a specific epithet that identifies which juniper species it is, such as western juniper (*Juniperus occidentalis*) or California juniper (*Juniperus californica*), etc. There are many species that have the genus name *Juniperus*, and many species that have the specific epithet *occidentalis* but only one *Juniperus occidentalis*. As you may have noted in this paragraph, species names are italicized and the genus name is capitalized while the specific epithet is not. The full formal name also includes the last name of the scientist who described the species and the year in which it was named. For example, the common limpets shown in Figure 6 carry the formal scientific name of *Patella vulgata* Linnaeus, 1758.



Figure 2.1.6: Common limpets, described by Carl Linnaeus in 1758 and named *Patella vulgata*. Image from Wikimedia Commons⁸.

Today, scientists have formalized guidelines they follow to choose names for new species. Scientists follow the guidelines of the [International Code of Zoological Nomenclature](#) (ICZN) or the [International Code of Nomenclature for Algae, Fungi and Plants](#) (ICN). These codes have strict rules for Latinizing names and descriptive terms to use in species names and for resolving conflicts in changes to scientific names. As our understanding of life on Earth expands, revisions to previous taxonomic groupings are often made and these guidelines help track changes and keep renaming or regrouping of organisms consistent.

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2.2: Measuring Species Diversity

How do we measure species diversity within a habitat? How do we compare diversity across different types of habitats containing very different numbers and types of organisms? There are many mathematical models that have been developed to quantify species diversity in different habitats. While these models differ in the exact method of diversity estimation, they all include two important components: species richness and species evenness.

Species richness is a measure of the number of different types of species in an ecosystem. A large number of different species in a habitat represents a higher species richness, and an overall more diverse ecosystem. **Species evenness** is a measure of the relative abundance of each species. More evenly represented species (evidenced by similar population sizes) illustrate a higher species evenness and an overall more diverse ecosystem.

Mathematically, we can distill species richness and species evenness of a habitat into a single measure of overall diversity using the following equation

$$D = (p_1^{-p_1})(p_2^{-p_2})(p_3^{-p_3}) \dots (p_n^{-p_n}) \quad (2.2.1)$$

where D is a measure of the total diversity of the ecosystem, and p_n is the proportion of species n . You will practice calculating D values and comparing diversity for different ecosystems in Lab 1: Discovering Diversity.

Exercise 2.2.1

For the following exercise, consider the four insect communities shown below.

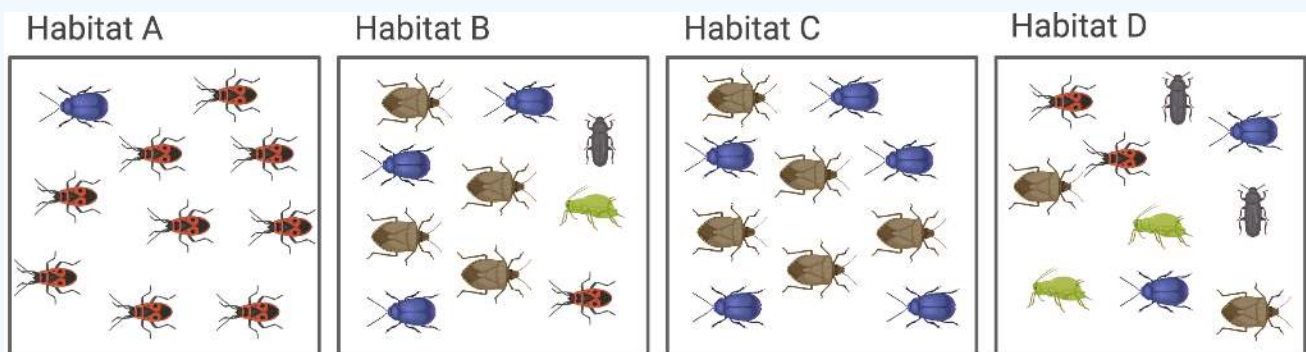


Figure created by L Gerhart-Barley with biorender.com

To determine the diversity value for a given habitat, we must first calculate the number and proportion of species in the habitat and then enter those numbers into the equation provided above.

Habitat A: Habitat A has two species, blue insects and red insects. There are 10 total insects in this habitat, 1 of which is blue and 9 of which are red. Consequently, the proportion of blue insects is $1/10$ or 0.1 and the proportion of red insects is $9/10$ or 0.9 . The D value for Habitat A is then

$$D = (0.1-0.1)(0.9-0.9) = 1.384$$

Calculate the diversity values for each of the other habitats to determine which habitat has the highest diversity.

Answer

$$\text{Habitat B: } D = (0.1-0.1) (0.1-0.1) (0.1-0.1) (0.3-0.3) (0.4-0.4) = 4.13$$

$$\text{Habitat C: } D = (0.5-0.5) (0.5-0.5) = 2$$

$$\text{Habitat D: } D = (0.2-0.2) (0.2-0.2) (0.2-0.2) (0.2-0.2) (0.2-0.2) = 5$$

Habitat D has the highest diversity

The methodology above is easy to use with small ecosystems that contain a small number of individuals and only a few species. Real ecosystems, however, are very large and can contain hundreds or thousands of species and tens of thousands of individual

individuals counted (rarefaction curve). In both cases, the researcher sampled the entire area shown in the map, which should result in a similar estimate of species diversity for the ecosystem. Which sampling method is used depends on the characteristics of the ecosystem and species to be sampled. You will practice sampling the diversity of an ecosystem and developing a rarefaction curve of your data in Lab 1: Discovering Diversity.

Earth's Biodiversity

How many species exist on Earth? This is a question that scientists have attempted to answer for centuries, beginning with Carl Linnaeus' first steps towards naming and classifying organisms in *Systema Naturae* in 1735. Linnaeus himself described over 12,000 species and in the nearly 300 years since, scientists have formally described and studied over a million more. Have scientists already discovered all, or most, of the species that live on Earth? If not, how many more remain to be discovered? These questions are inherently difficult to answer because they require us to estimate how much we *don't* know; how many species scientists have *not* discovered. This difficulty is compounded by the fact that certain regions of Earth and certain group of organisms have been much more heavily studied than others and so we know the diversity of organisms that is currently documented is somewhat biased.

Many studies have attempted to estimate the total biodiversity of Earth and, with varying methodologies, have produced estimates anywhere from 2 million to over 100 million species. Recently, [Dr. Camilo Mora](#) (at the [University of Hawai'i, Mānoa](#)) and his colleagues reviewed the various estimates and tested a new methodology to narrow down this large range to a plausible estimate. In the study, Mora used a similar strategy to the species-area and rarefaction curves described above; however, the estimate of 'effort' on the x-axis was not the area or number of individuals sampled, but time. Scientists have been described approximately 1.2 million species since the mid 1700's; has the number of new species described every year begun to level off? If so, that might indicate that most species have been discovered. If not, perhaps we can use the trend in new species discovered through time to predict where the graph might begin to level off. Mora's team also considered higher taxonomic levels; we can be relatively certain that scientists have not yet discovered every single species on Earth, but might scientists have already described all the genera, families, orders, classes, or phyla? The results of Mora's analysis are shown in Fig 3. By using the pattern of discovery of new organisms at different taxonomic levels (Fig 3A-F) and the relationship between maximum diversity of each level (Fig 3G), Mora's team arrived at an overall estimate of 8.7 million species on Earth. Since scientists have currently described approximately 1.2 million species, this estimate indicates that approximately 86% of species on Earth have not yet been discovered. At our current rate of discovery, Mora's team estimated that it will take scientists another 1,200 years to identify all species on Earth.



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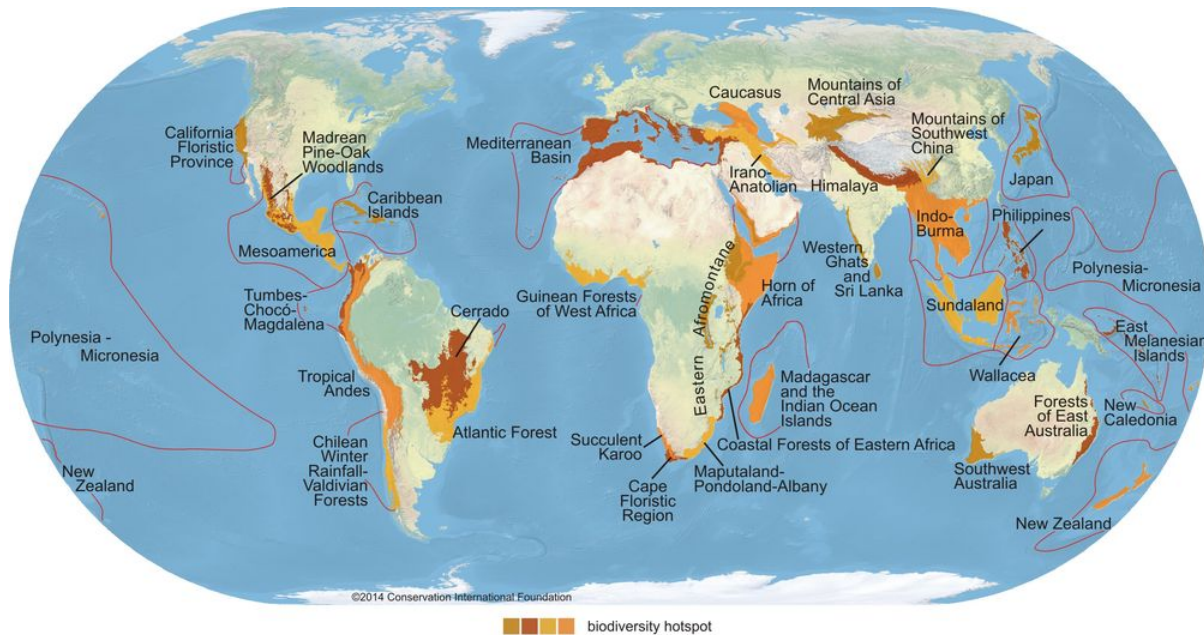
Figure from [Mora et al 2011](#).

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2.3: Patterns of Global Biodiversity

Biological diversity is not evenly distributed across the Earth; certain latitudes, ecosystems, and regions contain more diversity than others. There are several factors that influence how many species a given ecosystem supports and these factors lead to predictable patterns of diversity across the globe.

Some regions are deemed **biodiversity hotspots** (Fig 2.3.1); these regions contain more than 1,500 endemic (found only in that region) plant species and have lost at least 70% of their original area to anthropogenic uses (Myers et al 2000). Consequently, hotspots contain a high number of species that are unique to that ecosystem and which face serious conservation threats. The United States contains two biodiversity hotspots. The California Floristic Province stretches from southern Oregon to northern Baja Mexico, covers the majority of the state of California, contains ~2,125 endemic plant species and has lost over 75% of its area to agriculture and urban expansion. Nearly 40% of the Province is under federal protection to preserve the remaining biodiversity. The other biodiversity hotspot in the United States is the state of Hawai'i, which is part of the Polynesia-Micronesia hotspot incorporating the majority of the southern Pacific Ocean island systems.



Conservation International (conservation.org) defines 35 biodiversity hotspots — extraordinary places that harbor vast numbers of plant and animal species found nowhere else. All are heavily threatened by habitat loss and degradation, making their conservation crucial to protecting nature for the benefit of all life on Earth.

Figure 2.3.1: Biodiversity hotspots as described by Myers et al 2000 and expanded by Conservation International. Image from Wikimedia Commons¹.

Image Credit

1. https://commons.wikimedia.org/wiki/File:Biodiversity_Hotspots_Map.jpg

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2.4: Global Climate and Biodiversity

The **climate** of a region describes the average atmospheric conditions (temperature and precipitation) that region experiences and how much those conditions vary across seasons and years. Climate differs from **weather** in that weather is the atmospheric conditions at any given moment while climate is the long-term averages, patterns, or trends. This distinction is discussed in more detail in the chapter on climate change.

Climate is heavily influenced by the shape of the Earth, the tilt of the Earth's axis, and the pattern of the Earth's movement around the sun. First, the Earth is a sphere, which means that the intensity of the sun's energy varies across latitudes (Fig. 2.3.2). Near the geographic equator (0° latitude), the sun's rays hit the Earth directly, and deliver a high amount of heat and light per unit area. At high latitudes (nearer to the poles), the sun's rays strike the Earth at an oblique angle, and heat and light are spread across a larger area of the Earth's surface. Thus, the spherical shape of the Earth is responsible for the overall pattern of warmer average temperatures near the equator and cooler average temperatures towards the poles (Fig 2.3.3).

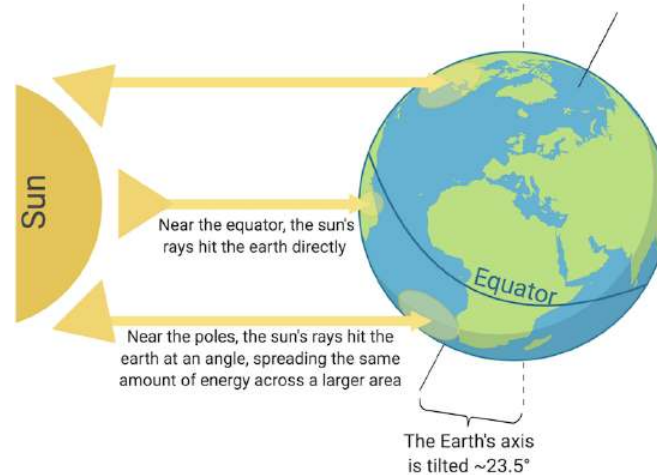


Figure created by L Gerhart-Barley with biorender.com

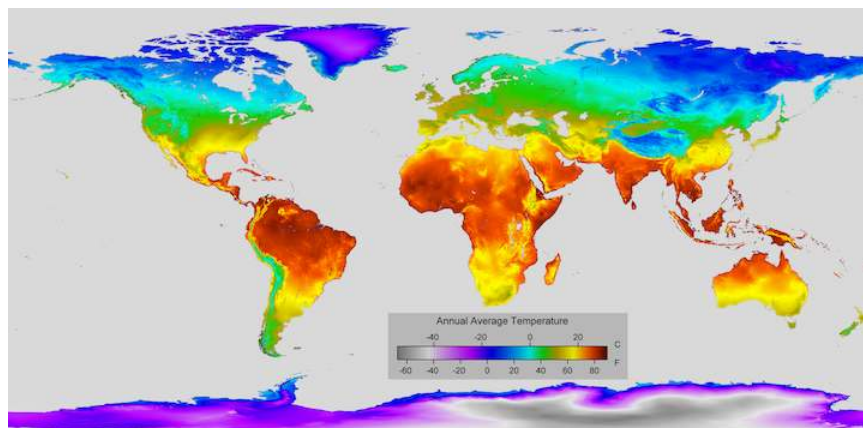


Figure 2.4.2: Global patterns of annual average temperature on land. Image from Wikimedia Commons¹.

Solar energy input also drives patterns of precipitation and atmospheric circulation (Fig 2.3.4). At the geographic equator, where the sun's energy is intense, the warm air expands and rises. As it reaches the upper atmosphere, it cools. Since cooler air cannot hold as much water vapor as warm air, these cooling, condensing air masses lose much of their moisture as precipitation. These air masses move away from the equator, towards the north or south. Around 30° N and S latitude, these cool, dry air masses fall back towards the surface of the Earth. As they approach the surface, they warm and absorb moisture back out of the lower atmosphere, causing dry regions around 30° N and 30° S latitudes. These air masses then move back towards the equator, where they will warm, absorb more moisture and rise again, completing the cycle of air movement between 0° (the geographic equator) and 30° N and 30° S (Fig 2.3.4). This cycle of air movement is named a **Hadley Cell**. Similar cells exist from 30° to 60° latitudes (called Ferrel Cells) and from 60° to 90° latitudes (called Polar Cells), though the Hadley Cell is the strongest, since it is centered where the sun's

energy is most intense. The spherical shape of the Earth, therefore, and its influence on these atmospheric cells, drives the overall pattern of global precipitation, particularly the abundantly high precipitation near the geographic equator and extremely low precipitation at 30°N and 30°S latitudes (Fig 2.3.5)

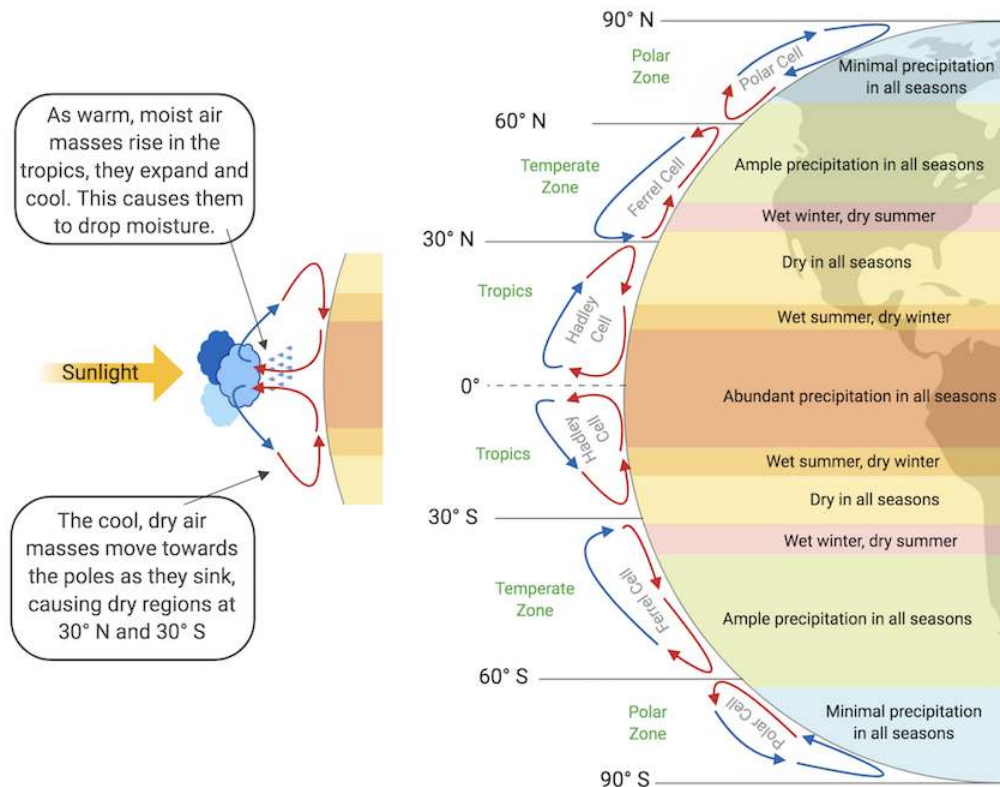


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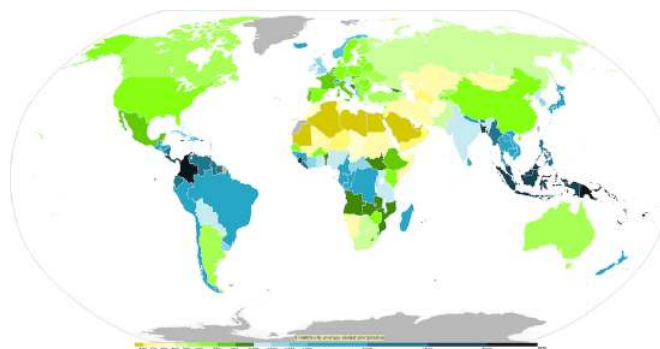


Figure 2.4.4: Global average annual precipitation for terrestrial ecosystems. Image from Wikimedia Commons².

As noted in Figure 2.3.2, the Earth's axis is tilted approximately 23.5° from vertical. The orientation of the axis stays constant as the Earth rotates around the sun meaning that the intensity of solar radiation a particular region receives varies throughout the year, producing seasons (Fig 2.3.6). In December, the Northern Hemisphere is tilted away from the sun and therefore receives less intense solar energy, while the Southern Hemisphere is tilted towards the sun and therefore receives more intense solar energy. Consequently, December is winter in the Northern Hemisphere and summer in the Southern Hemisphere. In June, the opposite is true; the Southern Hemisphere is tilted away from the sun and the Northern Hemisphere is tilted towards the sun. Consequently, June is summer in the Northern Hemisphere and winter in the Southern Hemisphere. In between these extremes, during September and March, are the seasons of fall and spring.

The tilt of the Earth's axis also causes changes in the day length, which are tied to the seasons; summer has longer days than winter.

December 21 and June 21 are the extremes for day length, called **solstices**. On December 21st, the Northern Hemisphere has its

shortest day (because it is angled away from the sun) and the Southern Hemisphere has its longest day (because it is angled towards the sun). Similarly, on June 21st, the Southern Hemisphere has its shortest day and the Northern Hemisphere has its longest day. The closer a region is to the pole, the greater the change in day length it will experience, such that regions north of the Arctic Circle ($\sim 66.5^\circ$ N) or south of the Antarctic Circle ($\sim 66.5^\circ$ S) fluctuate between 24-hour daylight at the summer solstice and 24-hour night in the winter solstice. Halfway between the solstices on September 21st and March 21st, day and night are of equal length, termed an **equinox**. The September equinox is autumn for the Northern Hemisphere and spring for the Southern Hemisphere. The March equinox is spring for the Northern Hemisphere and autumn for the Southern Hemisphere.

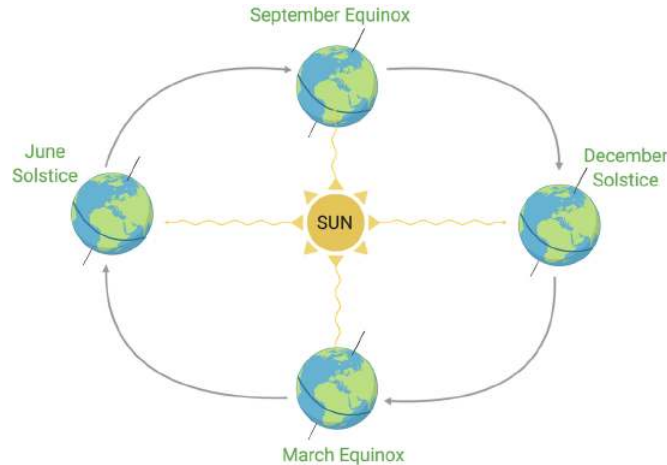


Figure 2.4.5: Relationship between the tilt of the Earth's axis and its orbit around the sun. Figure created by L Gerhart-Barley with biorender.com

Note

It is a common misconception that the seasons are driven by the distance of the Earth from the sun, with warmer seasons occurring when the Earth is close to the sun and cooler seasons occurring when the Earth is far from the sun. The distance of the Earth from the sun does not determine seasons. The pattern of seasons throughout the year is driven entirely by the tilt of the Earth's axis, which alters the intensity of solar radiation throughout the year. Warmer seasons occur when the solar energy is more intense and cooler seasons occur when solar energy is less intense.

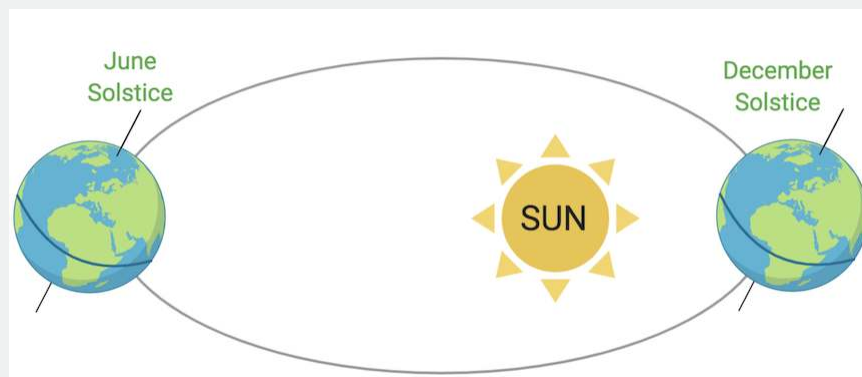


Figure created by L Gerhart-Barley with biorender.com

On average, the Earth is approximately 93 million miles from the Sun. This distance does vary a small amount due to the fact that the Earth's orbit around the sun is an ellipse, not a perfect circle, and the sun is not at the center of the ellipse. Consequently, at some parts of its orbit the Earth is closer to the sun than at other points in the orbit. The December solstice as shown in the figure above (2.4.6) is winter in the Northern Hemisphere because the solar intensity is lower, even though the Earth is closer to the sun at this part of the orbit. Similarly, the June solstice is summer in the Northern Hemisphere due to higher solar intensity, even though the Earth is further from the sun at this part of the orbit.

The Hadley Cell process illustrated in Figure 2.3.4 is centered where the sun's energy is most intense, termed the **thermal equator**. The geographic equator (0° latitude) does not move; however, the tilt of the Earth's axis and the Earth's orbit around the sun mean that the thermal equator is sometimes at the geographic equator and sometimes north or south of it. The movement of the thermal equator follows a predictable pattern that is linked with the seasons, solstices, and equinoxes described above. Each December solstice, the thermal equator is at its southern extreme. After the December solstice, the thermal equator begins moving north. It crosses the equator around the September equinox and continues moving north, reaching its northern extreme on the June solstice. After the June solstice, it begins moving south, crossing the equator during the March equinox and again reaching its southern extreme at the December solstice. Note that Figure 2.3.6 is not to scale and that the movement of the thermal equator is not as extreme as the figure implies.

The rainfall produced by the Hadley Cell air masses as they rise, expand, and cool produces a band of rainclouds, termed the **Inter-Tropical Convergence Zone (ITCZ)**. The ITCZ follows the thermal equator as it moves north and south throughout the year (Fig 2.3.8); however, since the ITCZ is in the upper atmosphere, it is also influenced by air currents and so does not always form a straight or solid band, and may even split into two bands in some seasons or in some areas.

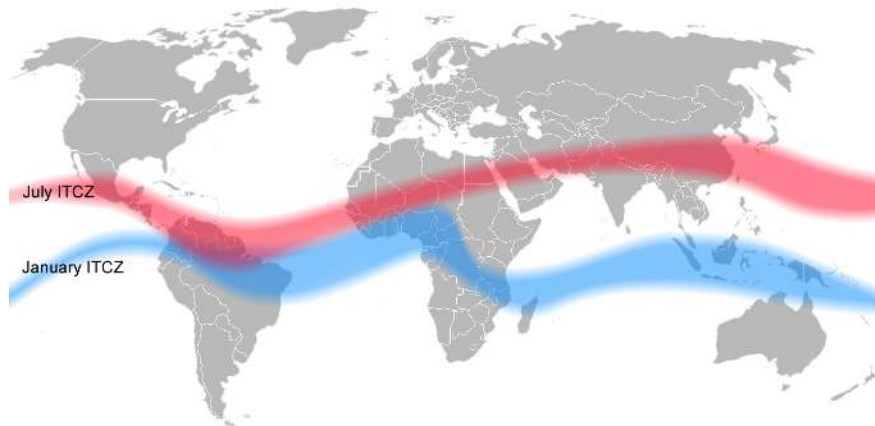


Figure 2.4.7: The location of the Inter-Tropical Convergence Zone (ITCZ) in July and January. Image from Wikimedia Commons³.

All the concepts discussed in this section are linked. The spherical shape of the Earth produces differences in solar intensity, and the maximum solar intensity occurs at the thermal equator. The center of the Hadley Cell is linked to the thermal equator, and the rising air masses at the center of the Hadley Cell form the ITCZ cloud bands, which are also then located roughly over the thermal equator (with some variation due to atmospheric currents). The operation of the Hadley Cell drives regions of intense rainfall at the center of the Cell, over the thermal equator, and regions of intense dryness at 30° N and 30° S latitude. The tilt of the Earth's axis and the orbit of the Earth around the sun cause the thermal equator (and therefore the center of the Hadley Cell and the ITCZ) to move north and south throughout the year, reaching its northern extreme during the June solstice and southern extreme at the December solstice, and being near the geographic equator (0° latitude) at the September and March equinoxes.

The global patterns of temperature (Fig 2.3.3) and precipitation (Fig 2.3.5) correlate to global patterns of biodiversity (Fig 2.3.9). Regions near the equator (which have high temperature and high precipitation) tend to have higher levels of diversity, while regions at higher latitudes (nearer to the poles) have overall lower diversity. This pattern is termed the **latitudinal diversity gradient**, and has been documented in many organismal groups, both terrestrial and aquatic. This gradient is discussed in more detail in the chapter on biomes.

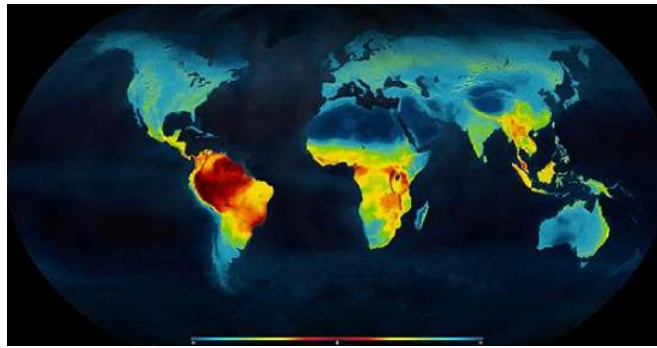


Figure 2.4.8: Global patterns of terrestrial vertebrate diversity. Image from Wikimedia Commons⁴.

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2.5: Earth's Geologic History and Biodiversity

Another global influence on biodiversity relates to patterns of geographic connectivity and isolation between regions throughout Earth's history. Recall that the Earth's crust is not one uniform piece, but instead split into several pieces, called **tectonic plates** (Fig 2.5.1). These plates are in motion (represented by the arrows on the map) and so have not always been located in the same place they are today.

 File:Tectonic plates boundary types & movement.png

Figure 2.5.1: The names, current locations, and direction of movement (arrows) of Earth's continental plates. Boundaries are color coded by type of plate movement; divergent (green), transform (black), and convergent (red, barred). Image from Wikimedia Commons¹.

Antonio Snider-Pelligrini (a French geographer) and Alfred Wegener (a German geophysicist) were early proponents of the idea of **continental drift**, the concept that continental plates move. In 1858, Snider-Pelligrini mapped how the South American and African continents may once have fit together. Wegener and Snider-Pelligrini then added to this map the locations of certain fossil species, which were found in regions that today are very distant from one another (Fig 2.5.2). Today, these areas are too far apart to believe one species could have migrated between them; however, the researchers proposed that these continents may once have been connected, allowing organisms to easily migrate between them.

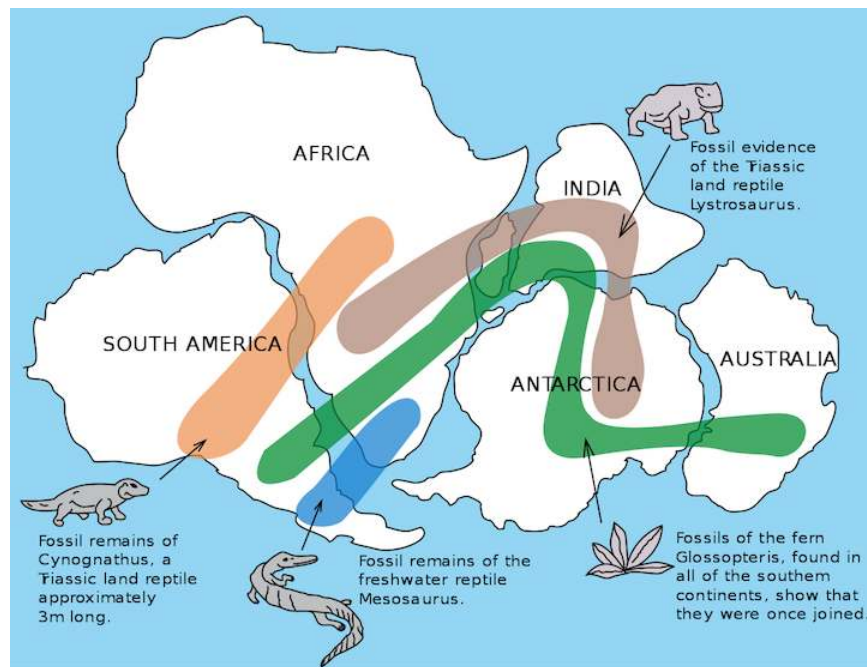


Figure 2.5.2: The Snider-Pelligrini/Wegener fossil map showing discoveries of fossils of the same species across South America, Africa, India, Antarctica, and Australia. Image from Wikimedia Commons².

As continents drift apart, the species that inhabit them may experience **vicariance**, which occurs when a species' geographic range is split into distinct regions separated by physical barriers the organisms cannot cross. In Figure 2.5.2, the species shown on the map were not able to cross the open ocean once the continents drifted apart. As we will see in future sections vicariance can play an important role in evolutionary change and speciation.

Patterns of vicariance throughout Earth's history can have profound impacts on biodiversity. For instance, up until about 3 million years ago, North and South America were separated by water in the region that today is Panama. As sea levels dropped, the land was exposed and connected the two continents, leading to what scientists call the Great American Biotic Interchange (Fig 2.5.3a), in which South American species like glyptodonts (Fig 2.5.3b) migrated north and North American species like mammoths (Fig 2.5.3c) migrated south. This connectivity between land masses led to a vast reassembly of terrestrial species in both continents and also caused a vicariant event for marine species. Previously, marine organisms had been able to migrate easily between the Caribbean and the Pacific Oceans; however, once the land bridge formed, populations on either side were separated from one another.

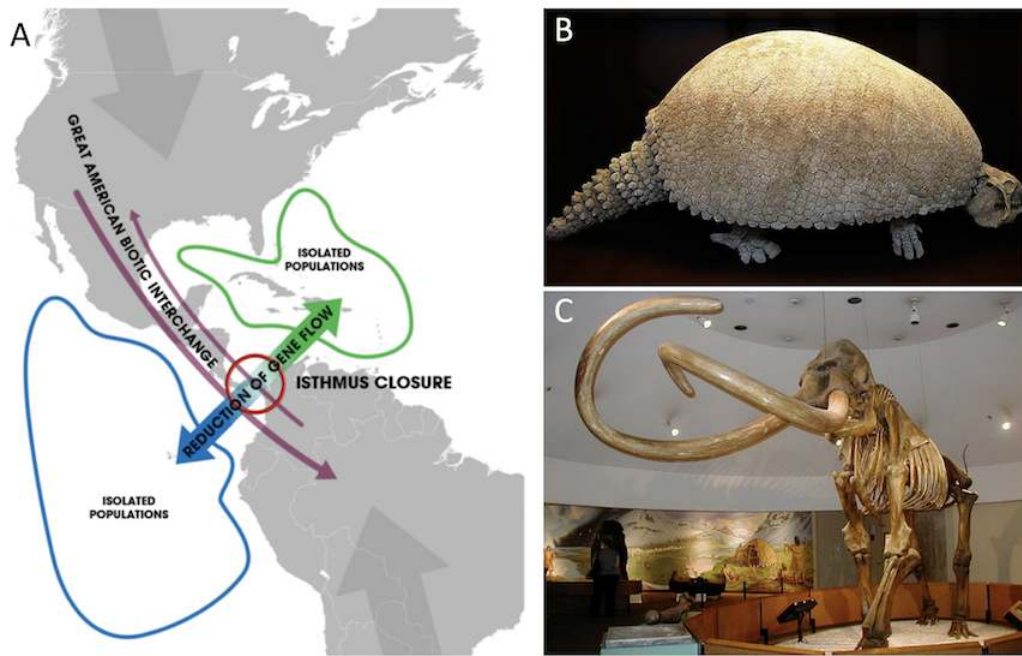


Figure 2.5.3: A) The impact of the formation of the Panamanian land bridge (located at the red circle) on terrestrial organisms in North and South America (purple arrows) and marine organisms in the Caribbean Ocean (green circle) and Pacific Ocean (blue circle). B) South American organisms such as this glyptodon were able to migrate north and C) North American organisms such as this mammoth were able to migrate south. All images from Wikimedia Commons^{3,4,5}

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2.6: Regional Topography and Biodiversity

The previous examples have shown how global factors can influence biodiversity, but it is important to note that regional factors on a smaller spatial scale than the entire globe can also strongly influence biodiversity. In this section, we will consider regional impacts of **topography**, the physical structure of the landscape, including mountains, valleys, etc. Consider, for example, the complex topography that results from California's numerous mountain ranges (Fig 2.6.1). Air masses moving across the California landscape must rise to go over these mountain ranges. As they rise, the air masses cool, expand, and drop much of their moisture as rainfall on the 'front' or windward side of the mountain range. When the air masses fall on the 'back' or leeward side of the mountain range, they are dry and so rainfall in this area is minimal. This process is called the **rainshadow effect** because the leeward side of the mountain ranges are 'shadowed' from receiving rainfall by the windward side of the range. Which side of a mountain range is the windward or leeward side depends on which direction the air masses are moving.

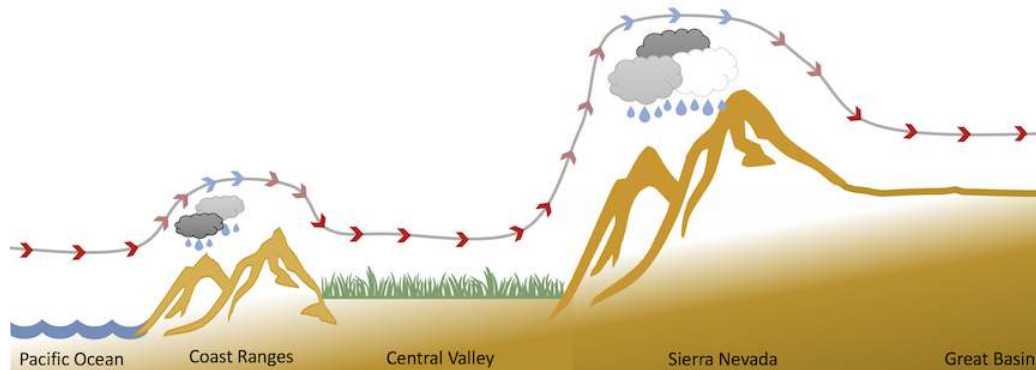


Figure 2.6.1: The rainshadow effect in California. Red arrows indicate warm air masses and blue arrows indicate cool air masses. Direction of arrows indicate direction of air movement. Image by L Gerhart-Barley.

In Northern California, air masses generally come from the Pacific Ocean and move east over the landscape (Fig 2.6.2). These air masses first rise over the coast ranges and deposit some rainfall on the western sides of these mountains. The central valley is in the rainshadow of the coast ranges and so receives less rainfall. The air masses then rise over the Sierra Nevada mountains, which are much taller than the coast ranges, and so the air masses deposit their remaining moisture on the western side of these mountains. Consequently, the great basin of Nevada is in the rainshadow of the Sierra Nevadas and is a desert, receiving very minimal rainfall. This pattern can be clearly seen in maps of the average annual precipitation of northern California (Fig 2.6.2)

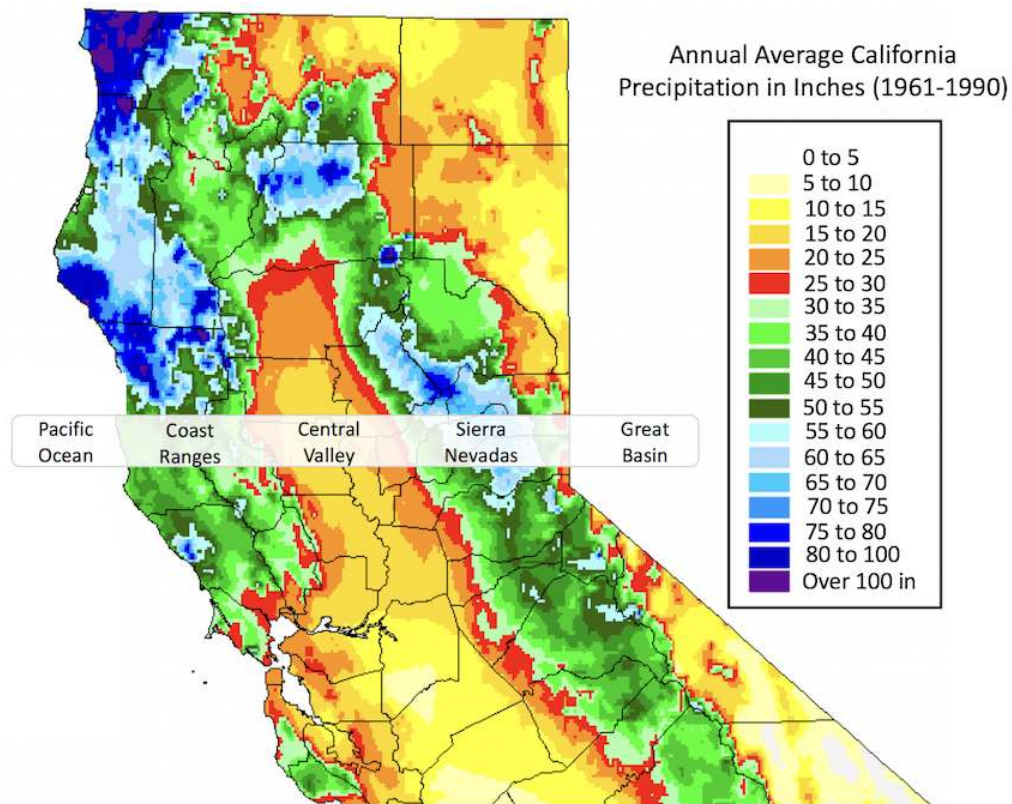


Figure 2.6.1 are labeled. Image from Wikimedia Commons¹.

The rainshadow effect influences biodiversity due to the influence it exerts on climate on the windward and leeward sides of mountains. The pattern of precipitation and elevation across a topographically complex landscape like northern California leads to differences in the plant and animal communities that inhabit these areas. For example, the western windward side of the coast ranges are famous for their redwood forests, while the eastern leeward sides are primarily oak forest. Similarly, the western windward side of the Sierra Nevadas are primarily mixed pine and fir forest, while the eastern leeward side contains a mix of juniper and pine woodlands, sagebrush scrub, and alkaline scrub systems as the landscape transitions to the desert flats of western Nevada. In both cases, the plant communities on the leeward side are more drought adapted than the communities on the windward side. The central valley between the coast ranges and Sierra Nevadas was historically grassland, though much of it has now been converted to agricultural and urban landscapes.

Image Credits

1. https://commons.wikimedia.org/wiki/File:North_California_Precipitations.gif

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2.7: The Value of Biodiversity

Global patterns and overall levels of biodiversity are important for a variety of reasons. Humans benefit directly and indirectly from biodiversity in many ways.

The Value of Biodiversity

Humans rely on a variety of products that are produced by plant and animal communities for food, clothing, shelter, medicine, textiles, and thousands of other products. These products are not only important for human sustenance and culture, but also a foundational component of many economies worldwide. Medicine in particular has greatly benefited from the discovery of therapeutic compounds discovered naturally-occurring in organisms. For example, the drug Taxol has been critical in treating cancer through its ability to disrupt the mitotic division of cancerous cells. This compound was discovered in the bark of yew trees, though in such low quantities that it would require cutting down a hundred different 100-year-old trees in order to treat a single patient. Fortunately, scientists were able to recreate the compound in the lab, allowing us to produce Taxol synthetically without having to cut down trees. Similarly, painkillers have been derived from the skin toxins of poison dart frogs, memory enhancers to treat Alzheimer's were isolated from the larvae of a marine bryozoans, diabetes medications were developed from venom in gila monster saliva, and perhaps the most famous, antibiotic compounds were discovered in moldy bread and used to produce penicillin (Fig 2.7.1).

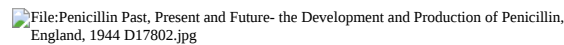


Figure 2.7.1: Alexander Fleming, the discoverer of penicillin, holds a petri dish containing the culture of bread mold from which the antibiotic compound was isolated. Image from Wikimedia Commons¹.

The discussion around medical advances from naturally-occurring compounds highlights another way in which humans benefit from biodiversity – scientific research. Pharmaceutical companies invest billions of dollars annually in research on therapeutic compounds, though there are many other ways that studying the diversity of organisms on earth benefits humans. The [National Science Foundation](#) funds \$6 billion worth of research grants every year, and even with that budget funds only ~5% of the grant proposals that are submitted to it by researchers. Much of this research is focused on better understanding how organisms operate, interact, evolve, etc and many of these studies have also led to advances in technology and medicine. For example, studies of how the structure of the peregrine falcon's nasal passages allow it to breathe while diving at upwards of 200 miles per hour led to advances in jet engine air flow design. Studies of the chemical composition of coral skeletons led to the development of new techniques for human bone grafts that reduce the patient's immune reaction to the graft. Studies of the adhesive compounds that allow mussels to cling to underwater surfaces led to the development of a non-toxic furniture glue, which replaced previous glues that had been found to be carcinogenic (cancer-causing). Several of these discoveries have received the [Golden Goose Award](#) from the [American Association for the Advancement of Science](#) (AAAS). These awards are chosen by AAAS to acknowledge federally-funded basic research that has led to important applications in biomedical research, medical treatments, and technology. Often, scientific research can seem obscure, esoteric, or even wasteful to the general public, yet these studies can lead to advances in medicine, technology, and other fields that benefit human health and society.

In addition to studying the natural world, many people enjoy experiencing nature and wild organisms on an emotional or personal level. Ecotourism is a booming industry; in the United States and Europe, adventure travel generates over \$260 billion annually. The [US National Park Service](#) reports that in 2018 alone, 318 million people visited a national park or national recreation area. Perhaps influencing this trend, recent studies have reported a calming or destressing effect from spending even a little time in nature, even a city park. The [UC Davis Arboretum and Public Garden](#) holds a series of nature-related relaxation events called [Nature Rx](#) (such as plein air yoga) as well as encouraging the use of [outdoor 'classroom' space](#) in the Arboretum, and outdoor exercise through the UC Davis [campus waking loops](#) (Fig 2.7.2).



Figure 2.7.2: Markers like this one are embedded in paths throughout the UC Davis campus to guide runners, walkers, and joggers along the various walking loop paths. Photo by L Gerhart-Barley

In addition to providing products, income, and aesthetic value directly to humans, diverse habitats support a number of other beneficial outcomes, collectively termed **ecosystem services**. These services include the food, medicine, and raw materials already described, as well as other important factors such as improving air and water quality, moderating disturbances such as coastal storm surges and flooding, preventing erosion and maintaining soil fertility, and providing breeding and nursery habitat for other species. Studies have shown that more diverse ecosystems are more stable (less responsive to disturbance), more productive (in terms of biomass produced), and provide more of the ecosystem services described above. We will return to this concept and discuss why higher diversity has these impacts in the section on ecosystem ecology.

More philosophically, biodiversity may also be seen as having intrinsic value, meaning that species have value simply due to the fact of their existence and not because of the services, products, or financial gain that humans can draw from them. A perspective of intrinsic value motivates many conservation organizations and environmental groups. UC Davis has several campus organizations dedicated to nature and the environment, including SEEDS, The Environmental Club, The Wildlife Society, and the Climate Action Project.

Threats to Biodiversity

Currently, biodiversity faces a number of serious factors that threaten the future of species on Earth. These threats include habitat alteration and destruction, introduced and invasive species, pollution, climate change, and overharvesting. Together, these threats have increased the rates of extinction and species loss to the point that scientists now report we are at early stages of a mass extinction event. Earth has experienced five mass extinction events throughout its history. The current 6th mass extinction is unique in that each of the factors listed above is anthropogenic (human-driven) in origin, meaning that we as a species are responsible for these extinctions. We will discuss the drivers and impacts of each of these threats throughout the quarter, starting with the next chapter on climate change.

Image Credit

1. https://commons.wikimedia.org/wiki/File:Penicillin_Past,_Present_and_Future-the_Development_and_Production_of_Penicillin,_England,_1944_D17802.jpg

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CHAPTER OVERVIEW

3: Climate Change

The **climate** of a region describes the average atmospheric conditions (temperature and precipitation) that region experiences and how much those conditions vary across seasons and years. Climate differs from **weather** in that weather is the atmospheric conditions at any given moment while climate is the long-term averages, patterns, or trends. To better understand the difference between climate and weather, imagine that you are planning an outdoor event to be held here in Davis. You might decide that July and August are not ideal for an outdoor event, since these months are usually very hot. You might also decide that December and January are not a good idea, since these months have the most rainfall in Davis. So perhaps you choose to hold the event in April predicting it will be not as hot as summer and not as rainy as winter. When you make this decision, you are thinking about climate. If you choose April 25th for the event, you cannot be certain that day will be cool and dry; however the climate of April in Davis suggests it is likely to be a good day for an outdoor event.

[3.1: Earth's Energy Budget](#)

[3.2: The Greenhouse Effect](#)

[3.3: The Cryosphere](#)

[3.3.1: Ice Sheets](#)

[3.3.2: Sea Ice](#)

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3.1: Earth's Energy Budget

To understand the global climate of Earth, it is important to understand the energy budget of the Earth, which drives the overall climate of the globe. The biodiversity section discusses how the sun's energy is unevenly distributed across the Earth's surface (which leads to the distribution of biomes and the pattern of the seasons); however, here we will consider the totality of energy the Earth receives from the sun across its entire surface (Fig 3.1.1). The majority of energy received from the sun (70%) is absorbed by the Earth's surface or atmosphere while the rest (30%) is reflected directly back out to space. The Earth's surface radiates a large amount of energy back up to the atmosphere (this value includes both the energy absorbed from the sun and the energy reabsorbed by the Earth's surface from the atmosphere), some of which is radiated back out to space, and much of which is retained in the atmosphere and reabsorbed by the Earth's surface.

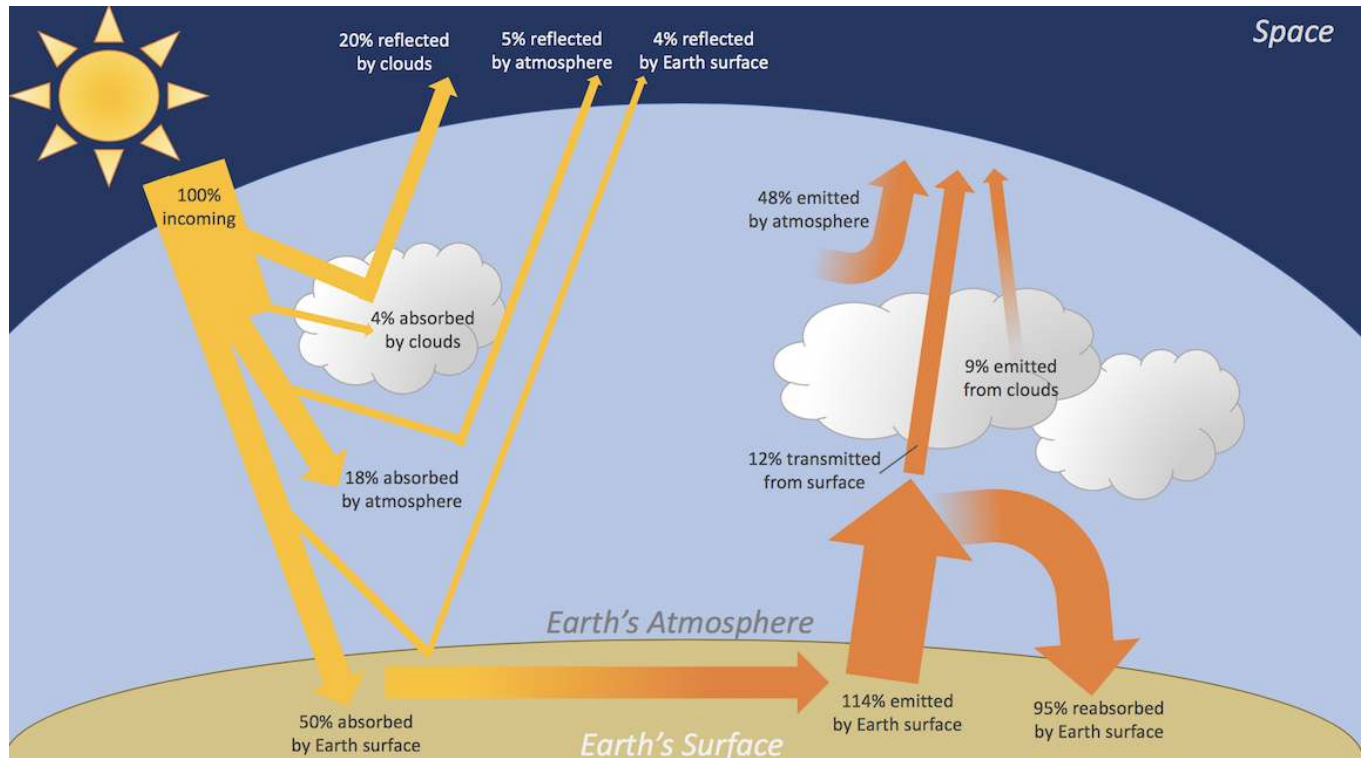


Figure by L Gerhart-Barley

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3.2: The Greenhouse Effect

The process by which the atmosphere absorbs the sun's energy and prevents it from being radiated back out to space has often been compared to that of a greenhouse, leading to the nickname the **greenhouse effect**. It is the same process that occurs when you leave your car sitting in the sun with the windows rolled up. The sun's rays are powerful enough to pass through the glass of the windows (or through the Earth's atmosphere) and be absorbed by the dashboard and seats (or the Earth's surface); however, when these surfaces emit energy, it is not powerful enough to pass back out through the window glass (or atmosphere) and in so doing becomes trapped within the car (or atmosphere) causing it to warm. There are certain atmospheric gases, termed **greenhouses gases (or GHGs)** that behave like the car windows, increasing the amount of energy retained in the atmosphere, and increasing the amount of warming that occurs. In Figure 3.1.1 the greenhouse effect is represented by the curved arrow showing 95% of the energy emitted by the Earth's surface that is reabsorbed, and the amount of GHGs in the atmosphere drive the size of this arrow.

The primary GHGs considered in this section are carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O). Scientists at the [National Oceanic and Atmospheric Administration \(NOAA\)](#) have been tracking concentrations of these and other GHGs in the atmosphere for decades (Fig 3.2.1) and have found that all three continue to steadily increase.

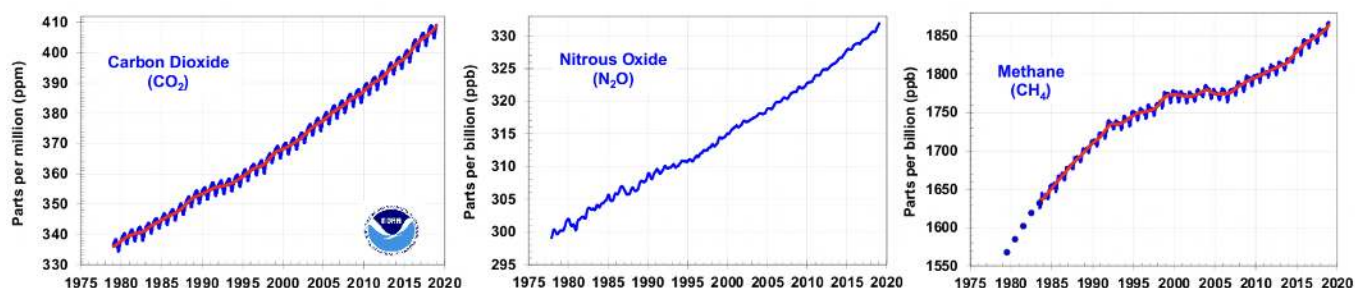


Figure 3.2.1: Global average concentrations of greenhouse gases carbon dioxide (CO_2), nitrous oxide (N_2O), and methane (CH_4) in the atmosphere since 1978. Image from NOAA¹.

These increases are particularly pronounced when compared to past GHG concentrations. Scientists can measure past atmospheric composition in ice sheets in Greenland and Antarctica. As the ice sheets formed, small bubbles of air were trapped in the ice, and coring deep into the ice sheet (Fig 3.2.2a) allows scientists to reconstruct atmospheric composition from direct measurements as far back as 800,000 years (Fig 3.2.2b). From these measurements, we can see that atmospheric CO_2 levels (and temperature, as estimated from oxygen isotope composition of the ice itself) have fluctuated significantly throughout the past. The ice sheets document a clear pattern of periodic increases and decreases in CO_2 , which are coupled with increases and decreases in temperature. Periods of low CO_2 and low temperatures are glacial periods (also referred to as 'ice ages'), and periods of high CO_2 and high temperature are inter-glacial periods. For the past 800,000 years, Earth has oscillated between glacial and inter-glacial periods roughly every 100,000 years. The maximum level that CO_2 concentrations reached in the last 800,000 years was approximately 300 parts per million (ppm). Global CO_2 levels are now over 400 ppm, a level that scientists estimate has not occurred on Earth since the Pliocene Epoch, approximately 3 million years ago.

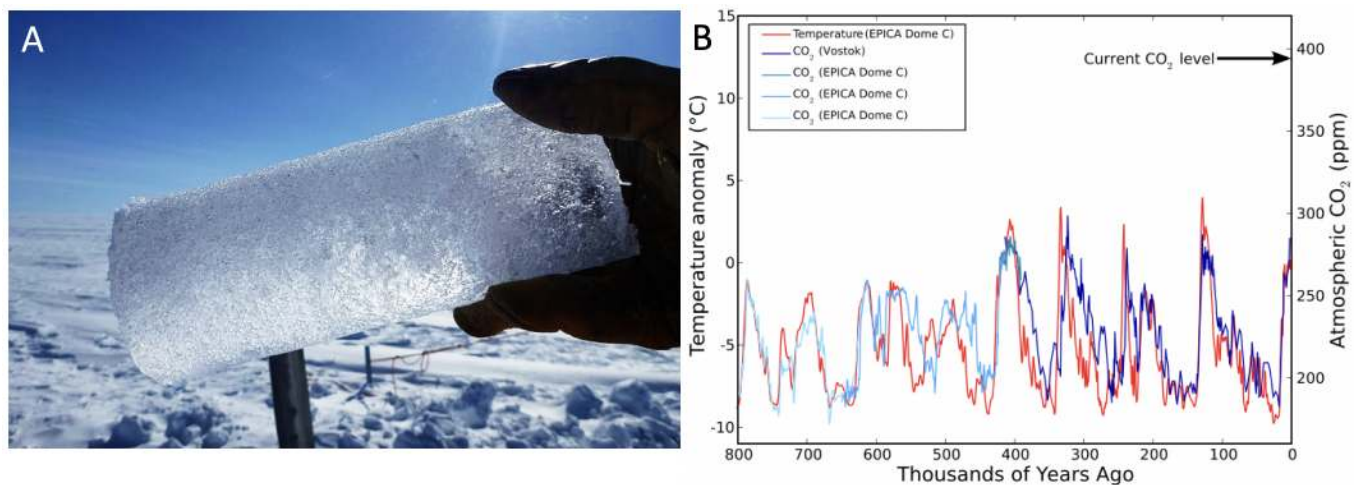


Figure 3.2.2: A) a section of ice core taken from the Greenland ice sheet and B) carbon dioxide concentration (blue) and temperature reconstruction (red) composites from EPICA Dome C ice cores (light blue and teal) in Greenland and Vostok ice cores (dark blue) in Antarctica. Global CO₂ level as of 2006 is marked with the 'Current CO₂ level' arrow. Images from Wikimedia Commons^{2,3}.

This increase in CO₂ (as well as other GHGs) increases the amount of solar energy that is retained in the atmosphere as opposed to radiated back out to space, which increases the temperature of the Earth's surface. Figure 3.2.3 shows the temperature anomaly for the decade 2014-2018 as compared to the average from 1951-1980. The [National Aeronautics and Space Administration](#) (NASA) reports that the global average temperature has increased approximately 1.4° Fahrenheit (0.8° C) since 1880, though that warming has not been evenly distributed across the Earth. As can be seen in Figure 3.2.3, the polar regions, particularly the Arctic, have warmed much more than other areas. This pattern is particularly concerning given the feedbacks that warming in polar regions may have on the melting of ice sheets and sea ice.

(2014-2018 Average vs 1951-1980 Baseline)

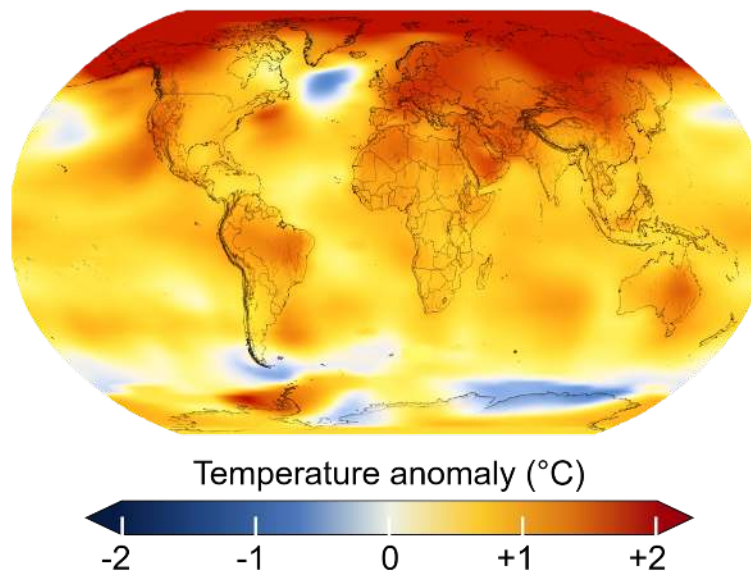


Figure 3.2.3: temperature anomaly for 2014-2018, compared to the average temperatures from 1951-1980. Image from Wikimedia Commons⁴.

In 2018, the state of California released its [Fourth Climate Change Assessment](#) report, which outlines the impact that global climatic changes are having and will have on the state (Fig 3.2.4). Some regions, most notably southern California, have already experienced nearly 3°F increases in annual average temperatures since the beginning of the 20th century.

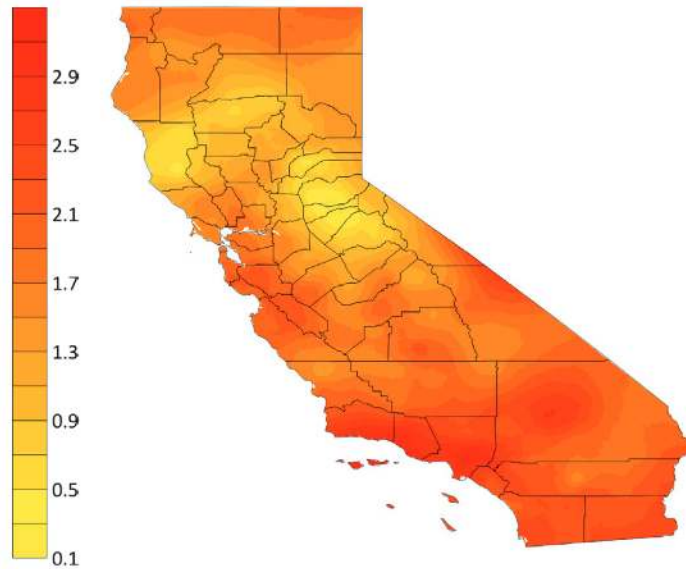


Figure 3.2.4 Observed changes in annual temperature across the state of California. Color bar represents the difference between the recent annual average temperature (1986-2016) and the annual average from 1901-1960 in degrees Fahrenheit. Positive values indicate recent averages are warmer than historical averages with higher values (darker red regions) experiencing more warming than lower values (yellow regions)

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- 1.
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SECTION OVERVIEW

3.3: The Cryosphere

The cryosphere (from the Greek kryos, meaning "cold", "frost" or "ice" and sphaira, meaning "globe") is all of Earth's water that exists in solid form, including ice sheets, glaciers, sea ice, and permafrost. Given its sensitivity to warming and the visibility of changes in ice extent, the cryosphere is an important component of climate change research and public communication on climate issues. This section will consider the physical changes to the cryosphere in response to warming temperatures across the globe.

3.3.1: Ice Sheets

3.3.2: Sea Ice

3.3.3: Glaciers

3.3.4: Permafrost

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3.3.1: Ice Sheets

Warming of the Earth's surface poses a particular threat for the Earth's ice systems including ice sheets, sea ice, permafrost (frozen ground), and glaciers. An ice sheet is a mass of glacial land ice that covers more than 50,000 square kilometers. Antarctica and Greenland hold the Earth's two ice sheets, and both lose hundreds of gigatonnes (109 tonnes) of ice mass each year to melting (Fig 3.3.1.1).

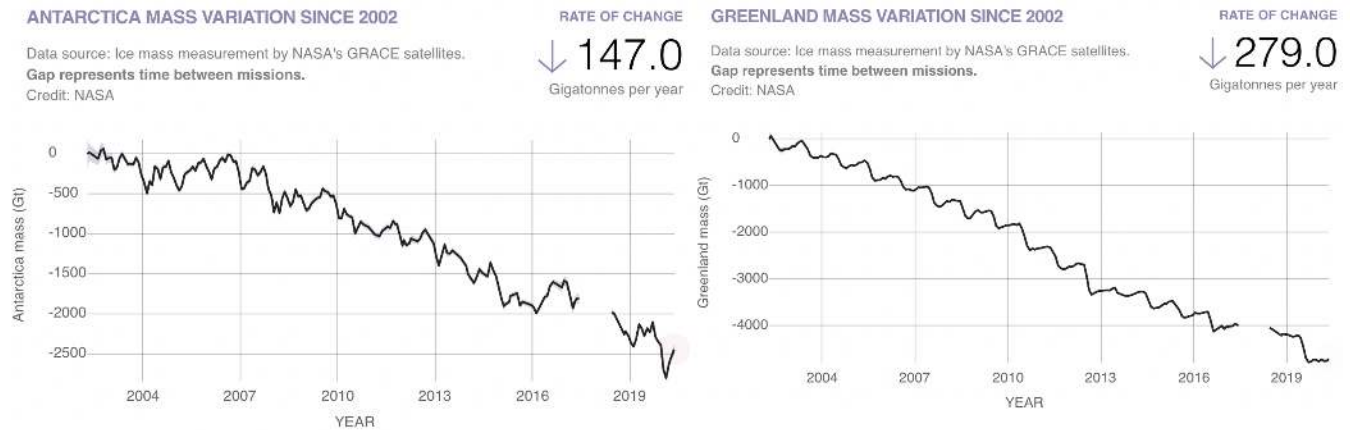


Figure 3.3.1.1: Mass loss in Antarctic (left) and Greenland (right) ice sheets due to warming. Images from NASA1.

In addition to persistent melting, the patterns of ice loss in Figure 3.3.1 lead to instability in portions of the ice sheets that can also result in major catastrophic events. A series of such events have occurred in the Larsen Ice Shelf on the Antarctic Peninsula. In ice shelf is a mass of ice that is anchored to land, but which juts out over the ocean, like a shelf. The Larsen A portion of the ice shelf collapsed and melted into the ocean in 1995. The Larsen B portion collapsed in 2002, dropping a sheet of ice the size of the US state of Rhode Island into the Southern Ocean, where it melted (Fig 3.3.1.2). In 2015, the Larsen C portion developed a 120-mile long crack from which, in 2017, a sheet of ice the size of the US state of Delaware collapsed into the Southern Ocean and melted.



Figure 3.3.1.2: The Larsen B ice shelf (left) in the Antarctic Peninsula with a scale comparison to the US state of Rhode Island which collapsed and melted into the Southern Ocean in February of 2002. The location of the Larsen A, B, and C shelves in the Antarctic Peninsula (right) prior to the collapse of portions B and C. Images from Wikimedia Commons2,3.

Recently, both Greenland and Antarctica have experienced short intense heat waves which have significantly increased localized melting. In July 2012, NASA's Earth Observatory [documented surface melting across 97% of the Greenland ice sheet](#) in response to a week-long heat wave. On June 18th 2019, Greenland experienced a 40 °F temperature increase which led to [massive surface warming](#) and an estimated loss of 11 billion tons of surface ice in a single day. Similarly, Antarctica set its highest temperature record of 65 °F on February 7th, 2020, leading to [significant ice loss](#) along the Antarctic peninsula, and associated islands, such as Eagle Island.

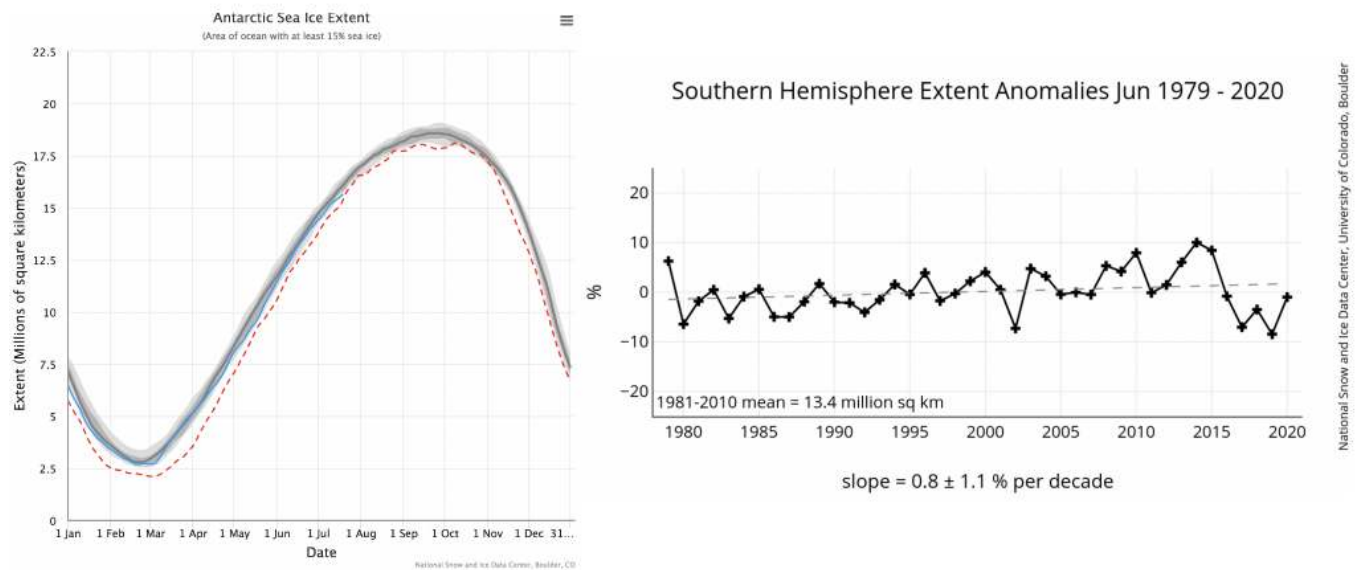
Image Credits

1. <https://climate.nasa.gov/vital-signs/ice-sheets/>
2. https://commons.wikimedia.org/wiki/File:Larsen_B_Collapse_Size_Comparison.png
3. <https://commons.wikimedia.org/wiki/File:Antarctic-Peninsula-Ice-Shelves.png>

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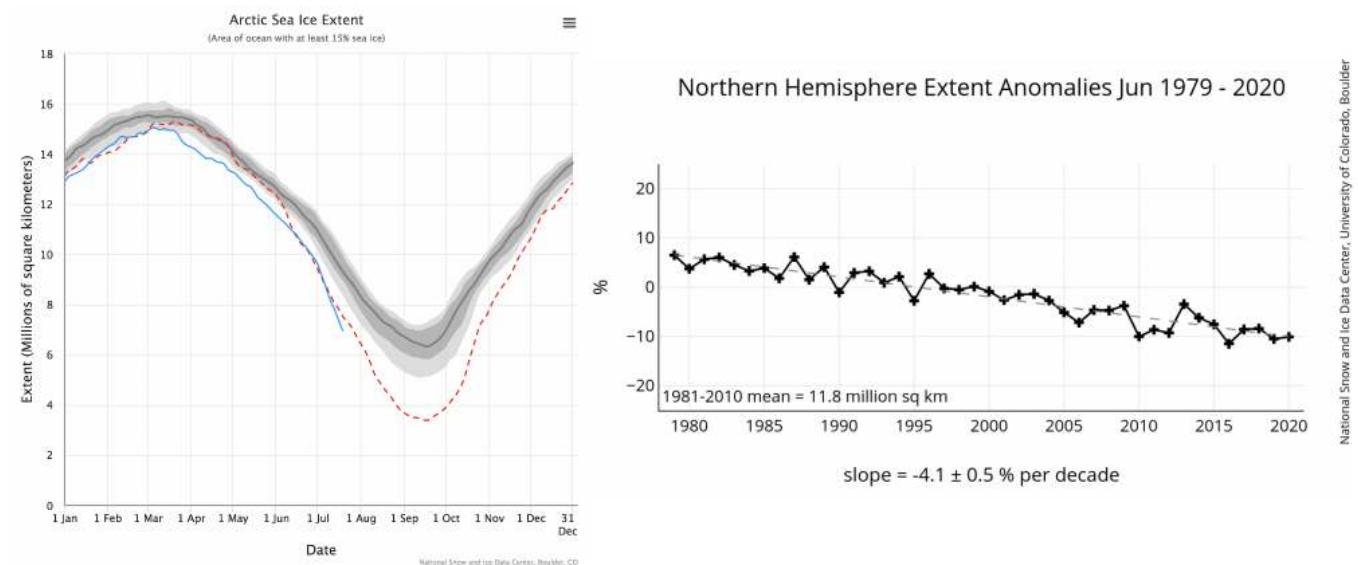
3.3.2: Sea Ice

In addition to land-based glaciers and ice sheets, the Arctic and Antarctic regions also contain sea ice, which is ice that forms over the open ocean and which often experiences large seasonal changes. Sea ice in Antarctica is relatively stable and experiencing minimal loss (**Fig 3.3.2.1**).



Figures from the National Snow and Ice Data Center¹

Sea ice in the Arctic Ocean is experiencing significant melting (**Fig 3.3.2.2**). Ice is very reflective and absorbs very little of the sun's energy; however, liquid water absorbs more than it reflects. Consequently, melting of sea ice leads to a feedback loop in which more open water leads to warmer surface water, which melts more ice and leads to more open water and more melting of sea ice.



Figures from the National Snow and Ice Data Center¹

The extent of sea ice loss in the Arctic Ocean is most clearly visible in the comparison between the record minimum year of 2012, and an average historical year, such as 1984 (Fig 3.3.2.3). Melting of sea ice in the Arctic Ocean is so severe that scientists predict the Arctic Ocean could be ice free in September by the year 2050.

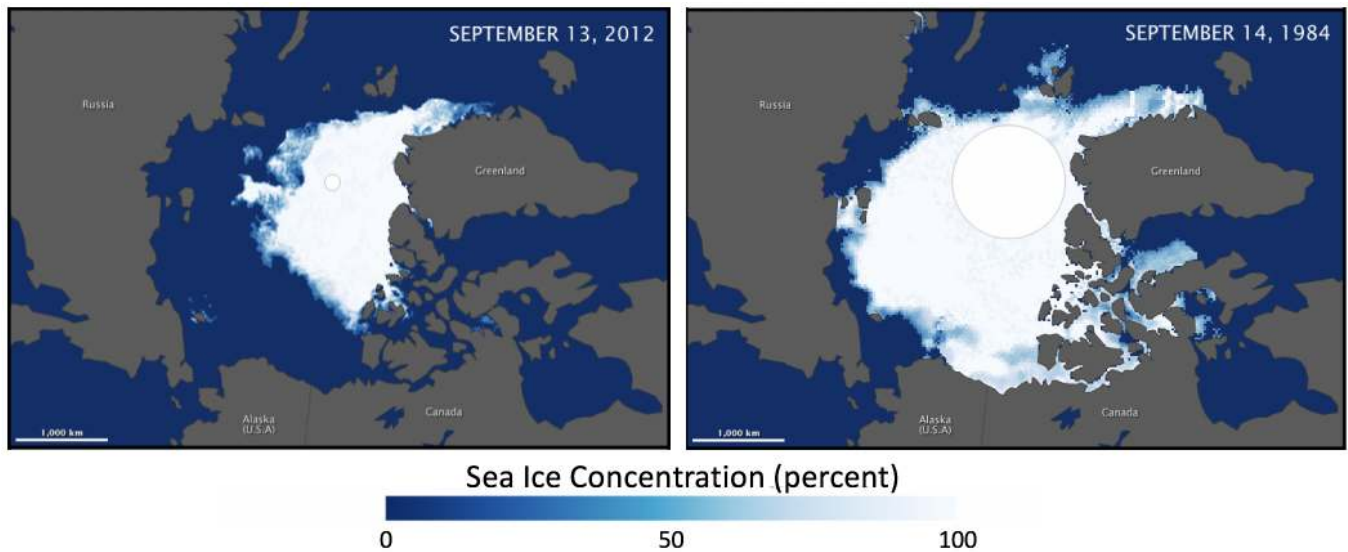


Figure 3.3.2.3: Extent of Arctic sea ice in September (annual minimum) in 2012 (left) and 1984 (right). Minimum extent in 1984 matched the overall average for the time period 1979-2000. White circles in the center of the ice indicate data gaps from the incomplete paths of satellites. Images from NASA2.

Image Credits

1. https://nsidc.org/data/seaice_index/
2. <https://earthobservatory.nasa.gov/images/79256/visualizing-the-2012-sea-ice-minimum>

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3.3.3: Glaciers

While ice sheets and sea ice are restricted to the poles, glaciers occur throughout the world, even in tropical locations, where mountain ranges reach elevations high enough to allow the development of ice. For example, both New Zealand and Chile contain high-elevation mountain glaciers. The [World Glacier Monitoring Service](#) (WGMS) tracks and reports data on ‘reference’ glaciers (glaciers with greater than 30 years of documented mass-balance measurements). Mass data on these reference glaciers indicates significant degrees of glacier mass loss across the globe (Fig 3.3.3.1).

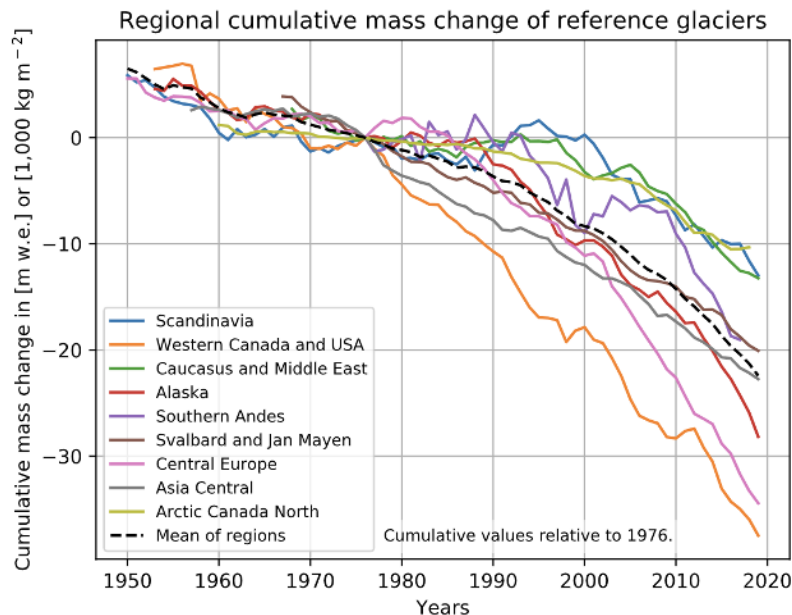


Figure 3.3.3.1: Cumulative glacier mass change for reference glaciers across the globe from 1950 to 2020 compared to each glacier’s mass value in 1976. Positive values indicate higher glacier mass, negative values indicate lower mass compared to 1976. Colored lines represent reference glaciers in different regions, while the black dotted line represents the global average across all regions. Image from WGMS 20201

In 1997, researchers at the [Northern Rocky Mountain Science Center](#) began the [Repeat Photography Project](#) to illustrate changes in glacier extent in [Glacier National Park](#), Montana, USA through current and historical photography. The value of this project is illustrated by the highly visible change in Grinnell Glacier from 1938 to 2015 (Fig 3.3.3.2). Warming and glacier melt is so severe in this region that a 2003 study estimated that the park may be ice-free, containing not a single glacier, by the year 2030 ([Hall and Fagre, 2003](#)), though other studies have predicted some glaciers may persist as long as 2080 ([Brown et al 2010](#)).



Figure 3.3.3.1: Ice loss in Grinnell Glacier in Glacier National Park, Montana USA. Images modified from USGS2.

Image Credits

1. WGMS (2020, updated, and earlier reports). Global Glacier Change Bulletin No. 3 (2016-2017). Zemp, M., Gärtner-Roer, I., Nussbaumer, S. U., Bannwart, J., Rastner, P., Paul, F., and Hoelzle, M. (eds.), ISC(WDS)/IUGG(IACS)/UNEP/UNESCO/WMO, World Glacier Monitoring Service, Zurich, Switzerland, 274 pp., publication based on database version: [doi:10.5904/wgms-fog-2019-12](https://doi.org/10.5904/wgms-fog-2019-12).
2. https://www.usgs.gov/centers/norock/science/grinnell-glacier-mount-gould?qt-science_center_objects=0#qt-science_center_objects

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3.3.4: Permafrost

Another important component of the cryosphere is permafrost, or frozen ground. The majority of permafrost is found in the Arctic (Fig 3.3.4.1), though the small area of land in Antarctica that is not covered by ice sheets also has permafrost. Regions containing permafrost are often categorized by the quantity of total area of the region that is frozen. Continuous permafrost, as its name implies is nearly entirely frozen with 90-100% of the land area of the region containing permafrost. Discontinuous permafrost, as the name implies, is not a single, solid sheet of frozen land (less than 90% of the total area is frozen), and can be sporadic (10-50% frozen area) or isolated (less than 10% frozen area).



Figure from the National Snow and Ice Data Center¹

As with other components of the cryosphere, permafrost is particularly sensitive to warming. One mechanism for tracking changes in permafrost extent is to measure the depth of the active layer, or the unfrozen soil that overlays permafrost. The [Circumpolar Active Layer Monitoring](#) (CALM) program tracks soil temperature and active layer depth in over 200 permafrost sites in both hemispheres. The resulting data on active layer depth for nine regions is shown in Fig 3.3.4.2 and indicates a consistent trend of soil warming, active layer depth, and permafrost loss across the Arctic.

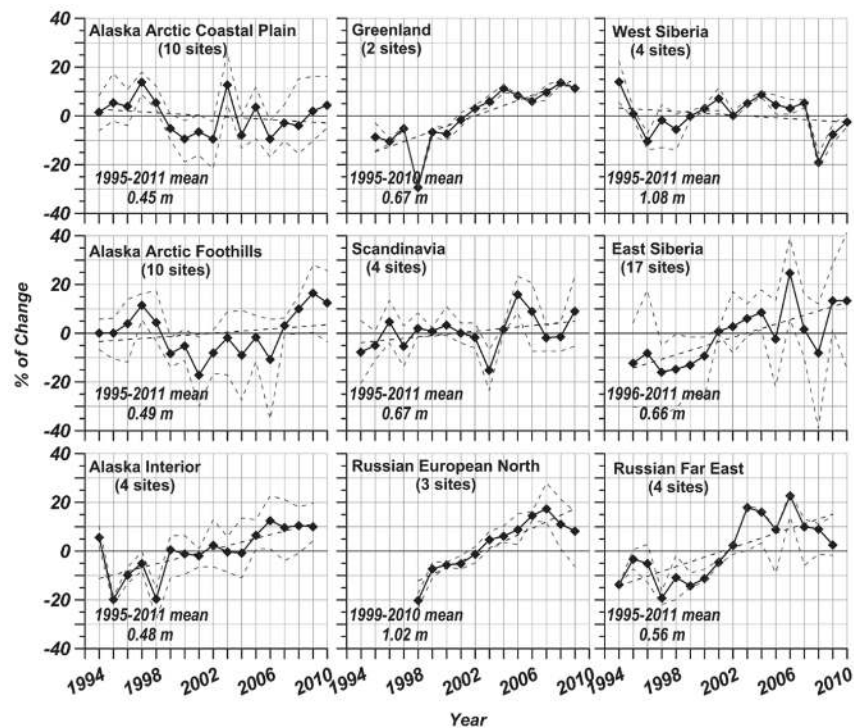


Figure from the 10th International Conference on Permafrost²

Degradation and thawing of permafrost has serious consequences for human communities and future climate change scenarios. Thawing of permafrost destabilizes soil profiles, which can lead to sinkholes, mudslides, and collapse of infrastructure built atop permafrost. Additionally, thawing of permafrost can directly release greenhouse gases that are frozen into the soil, and increases the respiratory activity of soil organisms, increasing the release of CO₂ in Arctic ecosystems. This represents a concerning feedback loop by which warming caused by atmospheric greenhouse gases leads to thawing of permafrost, which releases more greenhouse gases into the atmosphere, exacerbating warming trends and thawing of permafrost.

Image Credits

1. <https://nsidc.org/cryosphere/sotc/permafrost.html>
2. <https://ipa.arcticportal.org/meetings/international-conferences>

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3.4: Sea Level Rise

Much of the melting ice described previously contributes to sea level rise. The only exception is sea ice. Since sea ice is already floating in the ocean, its mass is already represented in the current sea level and so its melting does not affect sea levels. Think of a large glass of ice water, filled to the brim, and left sitting on a table – as the ice melts, the glass will not overflow because the mass of the water contained in the ice is already represented in the level of water in the glass.

Sea level rise has been documented throughout the globe (Figure 3.4.1) and is driven primarily by two factors: ice melt and warming. Warming of Earth's surface causes ice systems to melt, which increases the amount of water in the ocean and thus increases the sea level. In addition, warmer water takes up more space, since molecules expand as they are heated. Consequently, a warmer ocean will have a higher level due to thermal expansion of water molecules. Together, these two factors contribute the majority of sea level rise. Historically, the primary mode of long distance travel for both people and supplies was via water; consequently many of the world's major cities are coastal leading to serious concerns about rising sea levels and urban infrastructures. Additionally, low-lying island systems such as the South Pacific country of Vanuatu, whose mean elevation is less than a meter above sea level, are threatened with inundation as sea levels continue to rise.

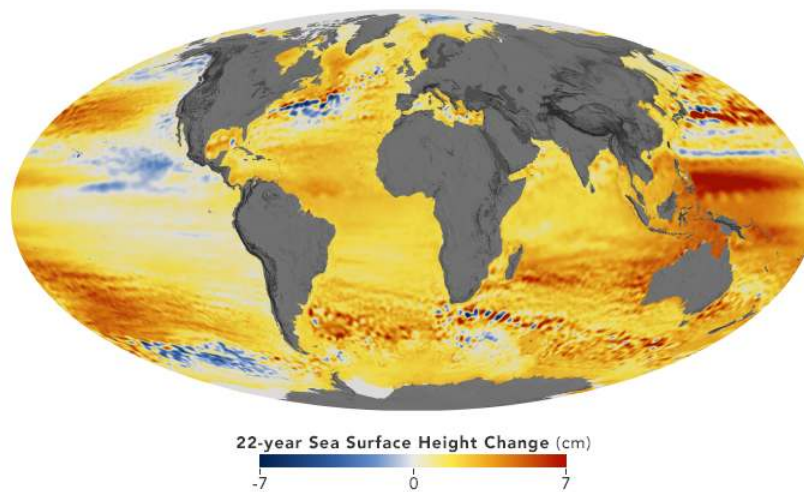


Figure 3.4.1: Sea surface height changes from 1992-2014. Image from NASA Earth Observatory¹

Image Credits

1. <https://earthobservatory.nasa.gov/images/91746/sea-level-rise-is-accelerating>

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3.5: The Future

With the data that have been gathered over the past 50-100 years on temperature, precipitation, ice melt, sea levels, and other factors related to climatic change, scientists can build models to represent the patterns that we have observed already and use these models to extrapolate predictions for what can be expected to occur in the near future. Frequently, scientists use multiple possible future scenarios, called Representative Concentration Pathways (RCPs) which are based on different choices that humans may make in the future and how these decisions affect future climatic change. RCPs differ primarily in the time period at which global GHG emissions peak and begin to decline and therefore how much warming we can expect. The commonly used RCPs are defined below:

- RCP 2.6: global annual GHG emissions peak 2010-2020
- RCP 4.5: global annual GHG emissions peak around 2040
- RCP 6.0: global annual GHG emissions peak around 2080
- RCP 8.5: global annual GHG emissions continue at their current level through the year 2100

Each RCP is named with a number that represents the difference in sunlight absorbed by the Earth's surface versus sunlight reflected back to space (discussed in Fig 3.1.1). Larger numbers represent a larger increase in absorption of sunlight and, therefore, more warming. The 'best case scenario', RCP 2.6, requires a peak-and-decline of global GHG emissions to occur by 2020; consequently, the best case scenario is no longer possible. The most extreme scenario currently used in the projections, RCP 8.5, assumes no major declines in GHG emissions until after the year 2100. This scenario is commonly referred to as 'business as usual.' Given the lack of binding international agreements which would limit or reduce future global GHG emissions, we are currently following RCP 8.5. Scientists can use the different RCPs to consider the impact of different global political decision making. As seen in Figure 3.5.1, the differences can be profound. These decisions matter, and the longer we as a global community take to respond to the threats of climate change and alter our GHG emissions, the more severe the ramifications will be.

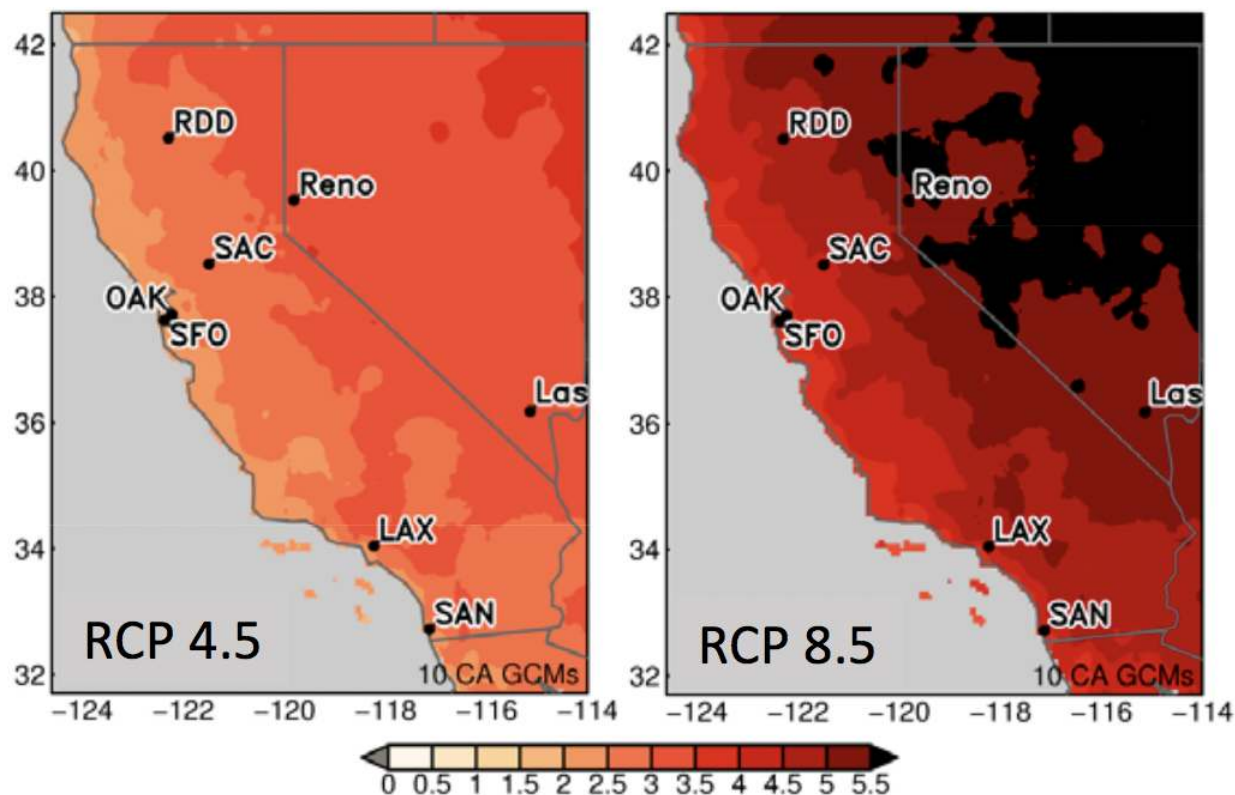


Figure 3.5.1: Projections for California maximum annual temperature for 2070-2100 under RCP 4.5 (left panel) and RCP 8.5 (right panel). Images from [Pierce et al 2019](#).

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CHAPTER OVERVIEW

4: Functional Diversity - Resource Acquisition

Scientists have estimated that there are ~8.7 million species on Earth. How does one planet support such enormous diversity of species? The answer relates to the impressive functional diversity (Fig 4.0.1) that organisms display – that is, the diversity in strategies and adaptations that different organisms have for surviving in their environment. The functional diversity sections address different strategies and adaptations for acquiring nutrients and resources from the environment, dealing with stressful environmental conditions (ex. heat stress), succeeding at or defending against predation, and successfully completing the life cycle.

This first chapter will focus on resource acquisition, particularly the two primary strategies for acquiring glucose (sugar) for respiration: autotrophy and heterotrophy. Autotrophs generate their own glucose through processes like photosynthesis. Heterotrophs acquire glucose by feeding on material in the environment. Both autotrophs and heterotrophs must obtain other nutrients besides glucose from the environment and have a wide variety of strategies and adaptations to do so. You will study a variety of resource acquisition strategies and their associated traits in Laboratory 2: Resource Acquisition in Eukaryotic Organisms.

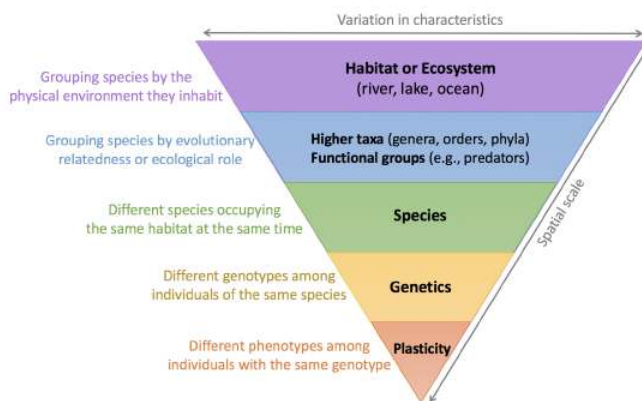
Figure 4.1: Schematic of the magnitude and type of diversity exhibited at different scales. This section focuses on functional group diversity. Figure by L Gerhart-Barley.

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[4.1: The Principle of Allocation](#)

[4.2: Resource Acquisition in Plants](#)

[4.3: Resource Acquisition in Animals](#)



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4.1: The Principle of Allocation

Functional diversity is driven the **Principle of Allocation** which states that each individual organism has a finite (limited) quantity of resources that it can use for all necessary life processes, including growth, reproduction, acquiring nutrients and resources, escaping predators or pathogens, etc. Resources such as nutrients or energy that an individual invests in one process cannot also be invested in other processes, meaning that not all life functions can be simultaneously maximized. This is sometimes referred to colloquially as a 'zero sum game' meaning that any increase in investment towards one process must be balanced by a reduction in the investment in another process, so that the sum of the changes is zero. You are already familiar with the principle of allocation through the concept of time. Each individual has 24 hours each day to invest in all the tasks that need to be accomplished. The more time a student invests in studying, for example, the less time is available for other tasks, such as sleeping.

The principle of allocation leads to trade-offs, which are the relationships between the benefits of resource investment decisions in one context compared to the costs of those decisions in another context. To use our previous example of time, investing more time in social activities may increase the number of friends you have (benefit), but will also decrease the amount of time available to study and likely result in lower grades (cost). Different species balance the principle of allocation and its associated trade-offs differently, resulting in a wide variety of strategies and traits that organisms use to accomplish life tasks. This variety of strategies and traits contributes to the diversity of species that exist on Earth.

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4.2: Resource Acquisition in Plants

Plants obtain the majority of the nutrients they need, including water, nitrogen, phosphorus, etc from the soil through their roots. The only exception is carbon, which is taken up in the form of CO_2 from the atmosphere.

Cation Exchange

Many of the nutrients that plants need from the soil are positively-charged ions, called **cations**. These include potassium (K^+), magnesium (Mg^{2+}), and calcium (Ca^{2+}). Soil particles often carry a negative charge, and so these compounds adhere to soil particles due to the attraction between opposite charges. In order for plant roots to take up these compounds, they must first be separated from the soil particles. Plants accomplish this separation through cation exchange (Figure 4.2.1). In cation exchange, the proton (H^+) concentration in the soil is increased in two ways. First, the root hairs exude H^+ ions directly into the soil. Second, respiration in root cells releases CO_2 into the soil, which reacts with soil water to form carbonic acid, which itself ionizes into bicarbonate and free protons:



The H^+ ions adhere more strongly to the negatively-charged soil particles than do mineral cations such as Mg^{2+} and Ca^{2+} . Consequently, the H^+ ions take the place of the mineral cations on the soil particles, leaving these compounds loose in the soil where they can be taken up by plant roots.

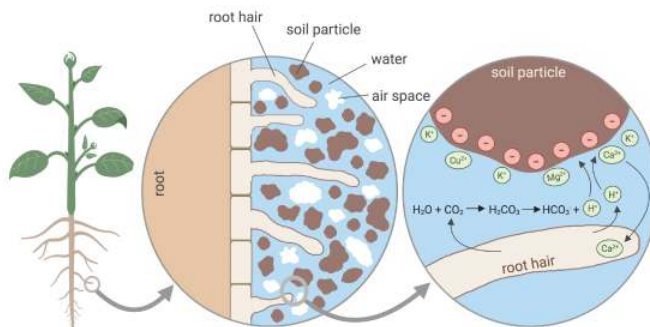


Figure 4.2.1: Diagram of the process of cation exchange mechanism for nutrient uptake. Image created by L Gerhart Barley with biorender.com

Root Mutualisms

In order to increase the quantity of nutrients obtained from the soil, plants have developed several mutualisms with other soil organisms. **Mutualism** is a type of species interaction in which both species benefit from the interaction. In this section, we will discuss two root mutualisms: mycorrhizae and root nodules.

Mycorrhizal relationships form between the roots of many plant species and a variety of soil fungi. Recall that the majority of the fungal body is in the form of branching filamentous structures called hyphae. In a mycorrhizal relationship, the hyphae of a fungus wrap around the root and/or penetrate the root. The plant root and the fungal hyphae can then exchange nutrients. Fungi are heterotrophs, so the fungus benefits by receiving glucose from the plant. Since many hyphae are microscopic and have a very high surface-area-to-volume ratio, they can access soil nutrients on a much finer scale than macroscopic plant roots. Consequently, the plant benefits by greatly increasing its ability to absorb nutrients of all kind throughout the soil, wherever the fungal body exists.

Mycorrhizal relationships fall into two broad categories: ectomycorrhizae and endomycorrhizae. Ectomycorrhizal fungi (Figure 4.2.2) form a sheath around the outside of the plant root and hyphae penetrate the root and wrap around the cell walls of individual root cells. Ectomycorrhizal relationships are common on woody plants, including trees. Endomycorrhizal fungi penetrate the cell walls of roots and grow between the cell walls and cell membranes of the root cells sometimes forming tree-like structures called arbuscules (Fig. 4.2.2). In both ecto- and endomycorrhizal relationships, the plant is able to access nutrients in any portion of the soil profile that contains the extensive fungal hyphae networks, significantly increasing the quantity of nutrients available to the plant. Some mycorrhizae specialize on providing particular nutrients (such as phosphorus) while the majority are generalists, providing any soil nutrients the plant requires in exchange for glucose from photosynthesis.

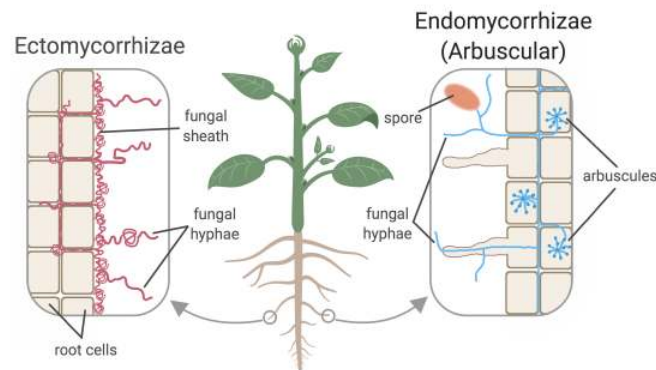


Figure 4.2.2: Diagram of ectomycorrhizal and arbuscular endomycorrhizal relationship between fungal hyphae and plant roots. Image created by L Gerhart-Barley with biorender.com

Root nodules are another form of root symbiosis. Root nodules form only between legumes (members of the plant family Fabaceae, including peas and beans) and a group of soil bacteria called **rhizobia**. This relationship is also mutualistic, though also more specialized than the mycorrhizal exchange. In this case, the heterotrophic rhizobia also receive glucose from the plant, and the plant receives nitrogen from the bacteria (Figure 4.2.3). Nitrogen is an important plant resource and is incredibly difficult for plants to obtain. Most nitrogen on Earth is in the form of N_2 gas in the atmosphere, which plants cannot use because of the powerful triple bond between the two nitrogen atoms, which renders it inert. Rhizobia bacteria are capable of converting N_2 into biologically useful forms (such as ammonium, NH_4^+), a process called nitrogen fixation. Unlike mycorrhizae, root nodules are macroscopic, and can be easily seen with the naked eye. You will study an example of root nodules in Lab 2: Resource Acquisition in Eukaryotic Organisms.

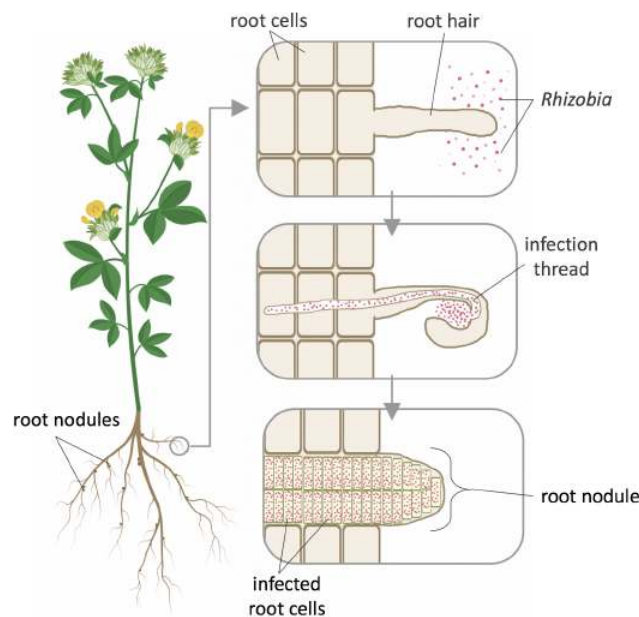


Figure 4.2.3: Diagram of the formation of root nodules between Rhizobia bacteria and legume roots. Rhizobia are present in the soil and infect root hairs of the plant, forming an infection thread the infiltrates root cells and forms a nodule. Image created by L Gerhart-Barley with biorender.com

Photosynthesis

At its simplest, photosynthesis is the process by which plants use light energy and CO_2 from the atmosphere to build glucose (sugar) molecules. Glucose is an energy storage molecule, and later breakdown of glucose in respiration will release the stored energy, making it available for the plant to use for growth, reproduction, etc.

Visible light contains wavelengths from 300-750 nanometers (nm) and plant leaves contain photosynthetic pigments that absorb portions of the visible spectrum. The three most common photosynthetic pigments are Chlorophyll A, Chlorophyll B, and

carotenoids such as beta-carotene (Figure 4.2.4). These pigments absorb wavelengths in the dark green and blue ranges as well as orange and red. They reflect yellows and greens, which is why most plants appear greenish in color.

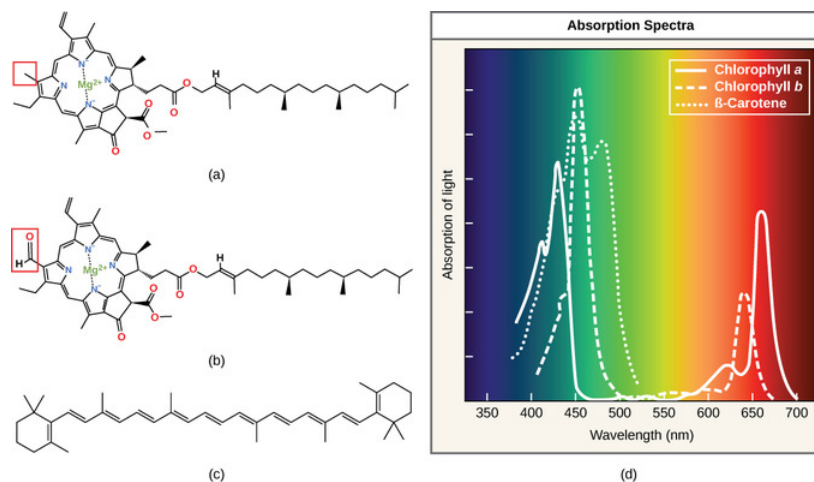


Figure 4.2.4: Chemical structure of Chlorophyll A, Chlorophyll B, and beta-carotene (A-C) and the absorption spectrum for each compound (D). Image from Wikimedia Commons¹.

Recall that photosynthesis is made up of two stages: the reactions in which light energy is absorbed by pigments and stored in short-term energy molecules such as adenosine triphosphate (ATP) and NADPH; and the reactions which use those energy molecules to power CO_2 uptake and its conversion to glucose (Figure 4.2.5). In this text, we will refer to the first set of reactions as the light energy harvesting reactions, though they are also sometimes called the light-dependent reactions, or simply the light reactions. We will refer to the second set of reactions as the glucose-generating reactions, though they are also sometimes called the light-independent reactions or the Calvin(-Benson) Cycle. We consider the names "light energy harvesting reactions" and "glucose-generating reactions" to be more accurate and descriptive. For example, the glucose generating reactions are not truly independent of light, as they rely on energy stored in the form of ATP and NADPH by the light energy-harvesting reactions.

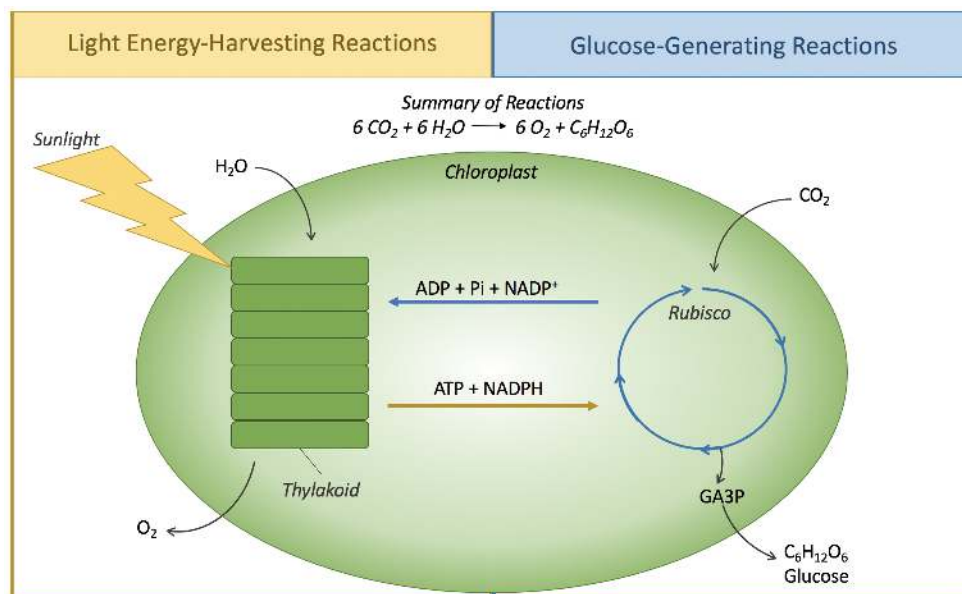


Figure 4.2.5: Overview of photosynthesis. Image by L Gerhart Barley.

There are three different 'types' of photosynthesis, termed pathways. The most common photosynthetic pathway is the **C3 pathway** (Figure 4.2.6), so named because the product of the first reaction is a 3-carbon molecule. Approximately 85% of all plants on Earth perform C3 photosynthesis and it was the first photosynthetic pathway to evolve, appearing on Earth about 2.5 billion years ago. In the C3 pathway, all mesophyll cells in the leaf perform photosynthesis. Mesophyll cells include all cells that are not vascular tissue (the leaf 'veins') or epidermal tissue (the outer layer of cells on the leaf surface).

Cross Section of C3 Leaf

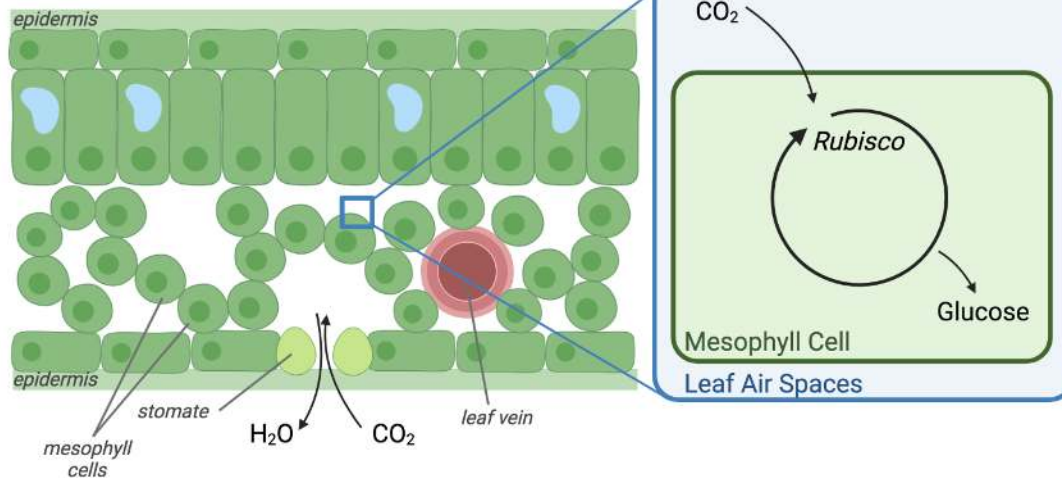


Figure 4.2.6: Diagram of the C3 photosynthetic pathway. Figure by L Gerhart-Barley using biorender.com

The C3 pathway has two major costs. The first cost is water loss: in order to get CO₂ from the atmosphere into the leaf, where it can be taken up by the mesophyll cells for photosynthesis, the leaf must open its **stomata** (pores in the epidermis). Anytime the stomata are open, water evaporates out of the leaf tissues to the atmosphere. Most of the water a plant obtains from the soil is lost this way. The second cost is a process called **photorespiration**, so named because it consumes O₂ and produces CO₂ (like respiration) and because it involves the photosynthetic protein **Rubisco**. The molecule that takes up CO₂ from the air, named Rubisco, can also bind to O₂. When Rubisco binds oxygen instead of carbon dioxide, the chloroplast is still able to produce glucose, but at a much slower rate and at a much higher energetic cost. Various environmental conditions, such as temperature and CO₂ concentrations affect how much photorespiration occurs in a cell. Consequently, the C3 pathway is most beneficial under cool and wet environmental conditions and when CO₂ concentrations are high.

Plants that perform C4 photosynthesis have developed a mechanism to avoid these drawbacks to C3 photosynthesis. The **C4 pathway** (Figure 4.2.7) is named for the fact that the product of the first reaction is a 4-carbon molecule. C4 plants differ from C3 plants in that carbon fixation (when CO₂ is picked up from the air spaces of the leaf) and the Calvin Cycle (when CO₂ is converted into glucose) occur in different cells of the leaf. In C3 plants, carbon fixation and the Calvin Cycle occur in the same place and time – Rubisco obtains a CO₂ molecule from the leaf air space and commences the Calvin Cycle immediately. In C4 plants, mesophyll cells use the molecule PEP-C for carbon fixation, which then moves to bundle sheath cells, where Rubisco is held to complete the Calvin Cycle. In this way, C4 plants avoid photorespiration by highly concentrating CO₂ in the cells where Rubisco operates and by using PEP-C (which cannot bind to oxygen) for the first uptake of CO₂. Concentrating CO₂ in the bundle sheath cells also allows C4 plants to close their stomata when environmental conditions are hot or dry, allowing them to save water while still keeping their photosynthetic activity high. Moving CO₂ into the bundle sheath cells, however, operates against the concentration gradient and so requires energy. Consequently, every glucose molecule that a C4 plant generates costs 2 more ATP energy molecules than under C3 photosynthesis. The C4 pathway is therefore most advantageous in environments that have higher temperatures and drier conditions (though not extremely arid) than those that favor C3 plants. The concentration of CO₂ in bundle sheath cells also means that C4 plants perform better than C3 plants under low CO₂ concentrations.

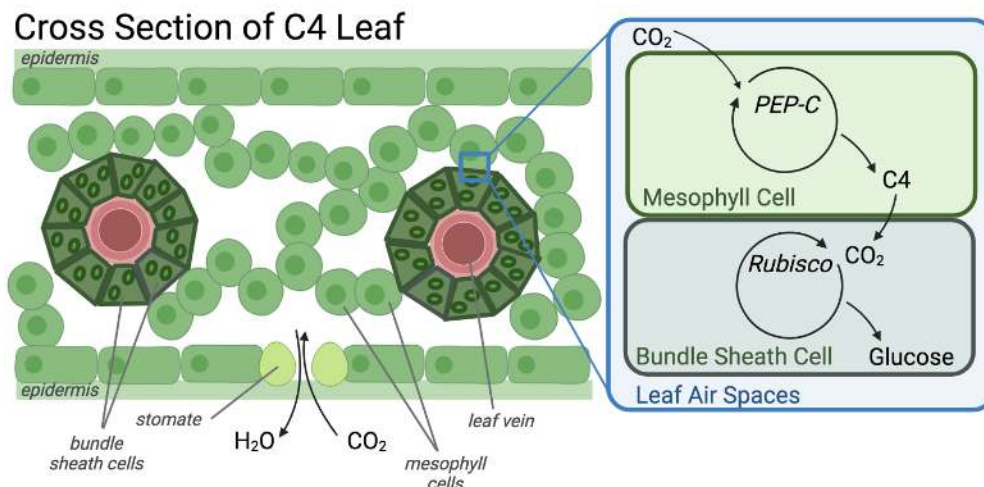


Figure 4.2.7: Diagram of the C4 photosynthetic pathway. Figure by L Gerhart-Barley with biorender.com

The third photosynthetic pathway is called CAM, an abbreviation of Crassulacean Acid Metabolism because this pathway was first discovered in the plant family Crassulaceae. Where C4 plants separate carbon fixation and the Calvin Cycle in space (where in the leaf they occur), CAM plants separate these processes in time (Fig 4.2.8). During the night, CAM plants use PEP-C to fix carbon, which is then converted to malic acid and stored overnight in the cell's vacuole. During the day, malic acid is taken out of vacuole and converted back into CO_2 , where Rubisco then completes the Calvin Cycle. This process allows CAM plants to keep their stomata closed during the day and only open at night, making it the most water efficient of the three pathways. Like C4 photosynthesis, however, the conversion of CO_2 to and from malic acid, and its storage in the vacuole overnight costs CAM plants two extra ATP energy molecules (compared to C3 photosynthesis) for every glucose molecule generated. In addition, having stomata open only at night reduces the amount of CO_2 CAM plants can fix, and so plants using this pathway tend to grow much more slowly than C3 or C4 plants. Consequently, CAM photosynthesis is generally only advantageous under conditions of extreme aridity, such as in deserts.

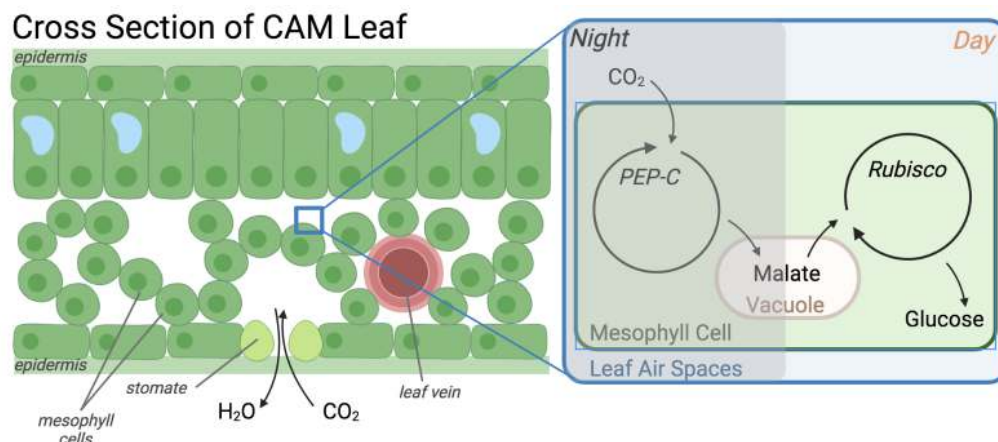


Figure 4.2.8: Diagram of the CAM photosynthetic pathway. Figure by L Gerhart-Barley with biorender.com

Limiting Nutrients and Growth Trade-Offs

Plants face particularly complex trade-offs when it comes to growth since investing in above-ground growth (leaves, stems, etc) reduces access to below-ground resources and vice versa. The availability of resources above ground (sunlight, CO_2) and below ground (water, other nutrients) consequently influences patterns of plant resource investment in growth. An important consideration in these trade-offs is which nutrient is most limiting for plant growth in a given environment. Justus von Liebig, a 19th century German chemist, developed an analogy to describe how varying nutrient levels influence plant growth. Liebig likened plant resources to a barrel made of wooden slats (Fig 4.2.9). Each slat represented a particular nutrient and the slat's height represented the relative availability of that nutrient in the ecosystem, compared to how much of that nutrient the plant needs (meaning that even if a nutrient is rare in the ecosystem, its slat may still be high if a plant requires very little of that nutrient). The quantity of water

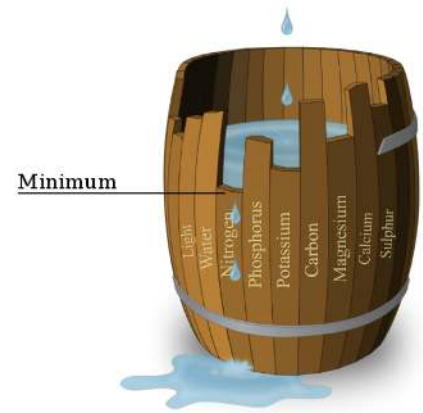
the barrel can hold represents plant growth in that ecosystem. The amount of water the barrel can hold is not driven by the height of the tallest slat, or even the average height of the slats; it is controlled entirely by the height of the shortest slat. Similarly, plant growth is not determined by the overall availability of resources, but by the availability of the limiting resource. The limiting resource is the resource that has the lowest availability compared to how much of that resource the plant requires (ie. the shortest slat). This concept is termed Liebig's Law of the Minimum because the resource with the minimum availability will determine plant growth in the ecosystem.

Figure 4.2.9: Diagram of Liebig's Law of the Minimum barrel analogy. Modified from Wikimedia Commons².

The slats in Fig 4.2.9 include above-ground and below-ground resources. Changes in the availability of resources above- or below-ground will influence plant investment in growth in these areas. Scientists discuss the balance of above- and below-ground growth in terms of the root-to-shoot ratio, abbreviated root:shoot. In this case, 'shoot' includes all above-ground growth including stems, leaves, and reproductive structures like flowers or cones. An increase in plant investment in below-ground growth (roots) will increase the root:shoot ratio while an increase in plant investment in above-ground growth (shoots) will decrease the root:shoot ratio. An increase in the availability of below-ground resources will lead the plant to invest more in above-ground tissues, causing a reduction in the root:shoot ratio. At first, this may sound counter-intuitive; however, if below-ground resources become more abundant, they are then relatively less limiting than above-ground resources and so the plant will be benefitted by increasing its investment in the above-ground resources by increasing its investment in shoot growth, which will reduce the plant's root:shoot ratio. The reverse is also true, if above-ground resources increase in availability.

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4.3: Resource Acquisition in Animals

Resource acquisition operates somewhat differently in animals than in plants. As heterotrophs, animals must consume all nutrients they require, including glucose. Animals have a variety of acquisition strategies available to them, depending on which trophic level and ecosystem they inhabit.

Types of Feeders

Animal resource acquisition strategies can be categorized in several ways. First, we might consider categorizing animals by what types of foods they eat. For example, herbivores consume plant material, carnivores consume animal material, and omnivores consume both. Each of these categories can be broken down more specifically. Among carnivores, there are piscivores which eat only fish and insectivores which eat only insects, as well as many other categories. Similarly, among herbivores, there are frugivores which eat only fruit, and granivores which eat only seeds, as well as many other categories. Another important grouping is the detritivores which consume detritus, or decaying dead plant and animal material. Detritivores are very important in nutrient cycling, and include organisms such as fungi, bacteria, earthworms, etc. Each of these strategies are associated with adaptations for increasing the effectiveness of that strategy. For example, herbivores often have symbiotic bacteria in their gut and particularly long intestinal tracts in order to break down the cellulose found in plant cell walls. Additionally, carnivores have a wide variety of adaptations for detecting, capturing, and consuming prey.

Animals can also be categorized by how they obtain the foods they consume. For examples, suspension or filter feeders filter particles of food from the surrounding water. Deposit feeders consume material deposited in the soil or sediment and are often also detritivores. Symbionts live in close association with another organism (their host) and obtain their nutrients from that organism. Symbionts can be parasitic (such as tapeworms) or mutualistic (such as the cellulose-digesting bacteria in the gut of herbivores). Perhaps the most well-known strategy for obtaining food is predation in which animals use stealth or active hunting to kill and consume other animals. This category can also be broken down into more specific strategies. For example, ambush predators use stealth and/or camouflage to hide from their prey and attack only when prey accidentally come near enough for the predator to capture or ambush. Spiders that hunt with webs are an example of ambush predators. Pursuit predators, however, actively chase fleeing prey. These two strategies have their own trade-offs; pursuit predation requires intensive energy investment in chasing down prey without guarantee of capture, while ambush predators must wait for potentially long time periods until prey come into their reach.

As can be seen in these definitions, various levels of specificity exist in both our definitions and in the strategies animals employ. Some animals are specialists, focusing on a particular strategy and/or food source. For example, pandas eat only bamboo and termites eat only wood (though from a variety of species). Other species are generalists and employ a wide variety of food sources and strategies. Bears, for example, are famous for their predation and also their love of berries. Goats and sharks notoriously eat things that are not even digestible food. The diets of many reptiles, such as lizards and snakes are what scientists call 'gape-limited' meaning they consume whatever fits inside their gaping mouths. Generalism and specialism have their own trade-offs. A specialist may struggle to find food that they can consume; however, they can also tailor their strategy to most effectively take advantage of a single food source. The anteater, for example, would have a difficult time consuming most types of prey, but is extremely effective at collecting ants. A generalist, on the other hand, can likely eat many things that it comes across in the ecosystem; however, it may not use those food sources as efficiently or effectively as a specialist.

Optimal Foraging Theory

Each food source and each consumption strategy have a balance of nutritional benefits and energetic costs. Ideally, an animal would choose food sources and strategies that maximize the nutritional benefits and minimize the energetic costs. Optimal foraging theory quantifies the benefits (in terms of energy content) of various prey choices and the costs (in terms of energy inputs for capturing, consuming, and digesting food) in order to predict the most energetically beneficial foraging choice. For example, consider a population of shore crabs (*Carcinus maenas*) that primarily feed on blue mussels (*Mytilus edulis*, Figure 4.3.1).



Figure 4.3.1: *Carcinus maenas* crabs (left) and their primary prey, blue mussels (*Mytilus edulis*). Images from Wikimedia Commons^{1,2}.

In order to consume the meat of the mussel, the crab must crack open its shell. Large mussels are more difficult to crack open, but contain more meat. Smaller crabs take more time and expend more energy in breaking open mussels than larger crabs. Consequently, what size of mussel provides the optimal energy return on the crab's energy investment depends on the size of the crab. Scientists quantified the amount of time it took for crabs of various sizes to crack open mussels of different size as well as the nutritional benefit of mussels of different size and used these data to estimate the value of different size of mussel prey for different sizes of predator crabs (Figure 4.3.2a). Scientists then tracked prey choice by crabs when presented with a variety of prey sizes and discovered that actual prey choice closely matched the patterns of prey value estimated by optimal foraging theory (Figure 4.3.2b).

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Figure 4.3.2: Figures from Valiela 19953.

Optimal foraging theory focuses entirely on energy costs of feeding and energy return from prey tissue consumed. Other environmental factors may drive predators to make choices different from what optimal foraging theory predicts. For example, if capturing high quality prey items exposes the predator themselves to danger (their own predators, for example), then animals may choose less energetically valuable prey in safer areas of the habitat. Additionally, some plants contain rare nutrients that herbivores require in their diet and so grazers may seek out these plants even if they are not energetically as beneficial.

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2. https://commons.wikimedia.org/wiki/Mytilus_edulis#/media/File:Miesmuscheln_Mytilus_1.jpg
3. https://link.springer.com/chapter/10.1007/978-1-4757-4125-4_6

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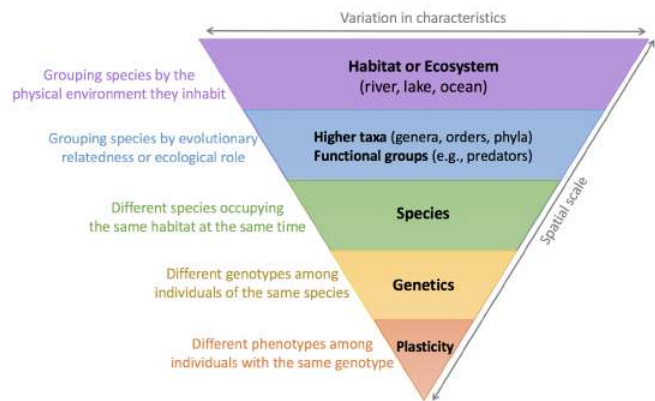
CHAPTER OVERVIEW

5: Functional Diversity - Stress and Enemies

Scientists have estimated that there are ~8.7 million species on Earth. How does one planet support such enormous diversity of species? The answer relates to the impressive functional diversity (Fig 5.0.1) that organisms display – that is, the diversity in strategies and adaptations that different organisms have for surviving in their environment. The functional diversity sections address different strategies and adaptations for acquiring nutrients and resources from the environment, dealing with stressful environmental conditions (ex. heat stress), succeeding at or defending against predation, and successfully completing the life cycle.

This second chapter will focus on strategies organisms use to deal with abiotic stressors (such as thermal stress) and biotic stressors (such as predation and parasitism) and how abiotic and biotic interactions shape an organism's niche.

Figure 5.1: Schematic of the magnitude and type of diversity exhibited at different scales. This section focuses on functional group diversity. Figure by L Gerhart-Barley.



[5.1: The Ecological Niche](#)

[5.2: Acclimation and Adaptation](#)

[5.3: Stress - Thermoregulation](#)

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5.1: The Ecological Niche

An important concept in ecology, which will be discussed in several contexts throughout the quarter is the ecological niche. A species' **ecological** niche is the abiotic and biotic conditions the species requires in order to grow, reproduce, and survive. Every species, therefore, has a fundamental niche, which are the abiotic conditions the species can physiologically tolerate, as well as a realized niche, which is driven by species interactions. For example, consider a species of fish living in the ocean (Fig 5.1.1).

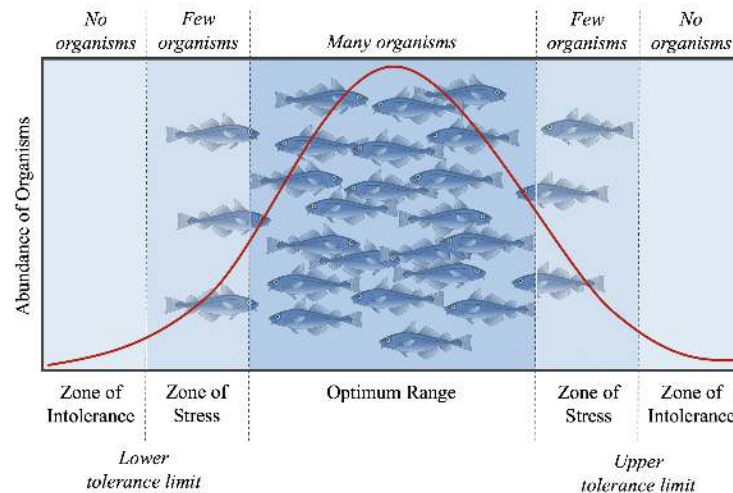


Figure 5.1.1: How tolerance ranges relate to organism abundance. Figure by L Gerhart-Barley

This species has certain physiological tolerances in temperature, salinity, etc, that determine where the species can exist. Each of the abiotic factors has an optimum range, where the species will be abundant. Outside of this optimum range (both above and below it), are zones of stress, where the species can survive, but experiences physiological stress and will be less common than in the optimum range. Beyond the zones of stress, are zones of intolerance, which represent conditions the species cannot tolerate and in which it will not be found. The tolerance ranges for all relevant abiotic conditions represent the species fundamental niche (Fig 5.1.2). Species interactions such as predation, parasitism, mutualisms, etc may result in this species not being found throughout its entire fundamental niche. For example, if this fish's prey species do not occur in some areas of the fundamental niche, then this fish species may not occur there even though it could physiologically tolerate these conditions.

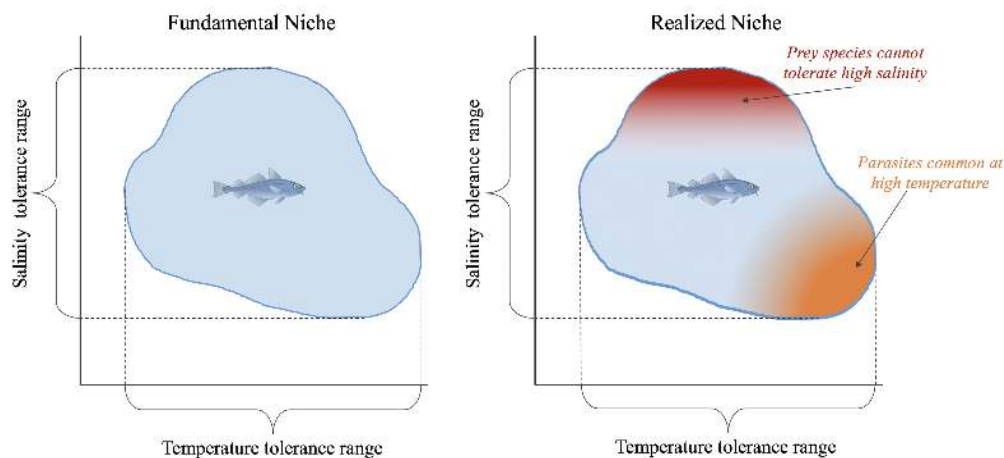


Figure 5.1.2: The relationship between the fundamental niche (based on abiotic tolerance limits) and the realized niche (based on species interactions) for a fictional fish species. Figure by L Gerhart-Barley

The example above illustrates how a species' realized niche might be reduced or contracted compared to the fundamental niche; however, species interactions can also expand the realized niche. For example, the resource acquisition section discussed root mutualisms that many plants form with mycorrhizal fungi and *Rhizobium* bacteria, which help the plant access soil nutrients. These mutualisms can expand the minimum soil nutrient availability in which the plant can survive, expanding its fundamental niche (Fig 5.1.3). We will consider the impact of species interactions on the niche in more detail in the species interactions sections.

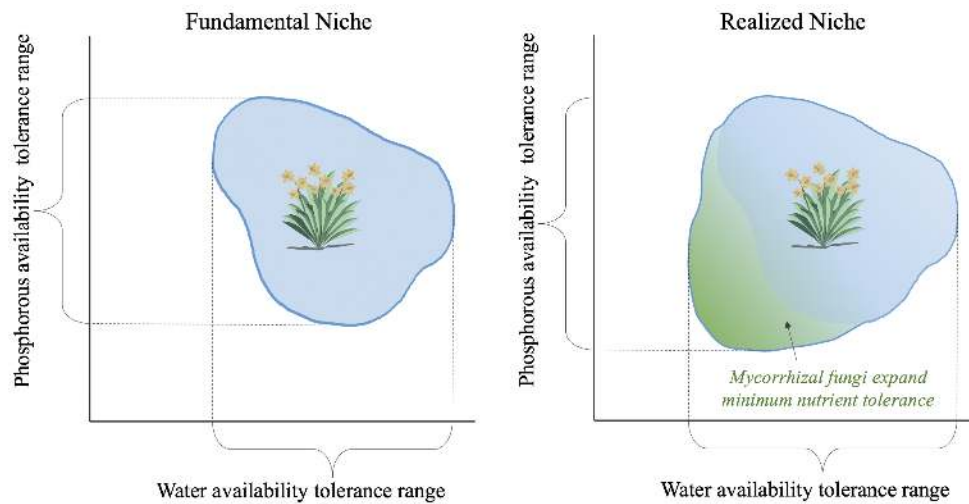


Figure 5.1.3: The relationship between the fundamental niche (based on abiotic tolerance limits) and the realized niche (based on species interactions) for a fictional plant species. Figure by L Gerhart-Barley

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5.2: Acclimation and Adaptation

Species respond to environmental stressors through acclimation and adaptation. The distinction between the two is important; though they are linked, they operate at very different scales and with different short-term and long-term ramifications. **Acclimation** occurs when an individual organism experiences a change in its phenotype in response to an environmental stressor. This change is reversible and occurs very rapidly, sometimes in as little as a few minutes. **Adaptation** occurs when a population experiences a change in its genotype in response to an environmental stressor. This change occurs much more slowly, usually across many generations, and is a result of natural selection.

For example, imagine you set out to hike to the summit of Mt. Whitney in California's [Sequoia National Park](#). The peak is approximately 14,505 feet (~4420 meters) in elevation; high enough that the air is much thinner at the top (Fig 5.2.1) and therefore your lungs will struggle to obtain the oxygen necessary for you to breathe. As you hike higher and higher in elevation, your body will acclimate by producing more hemoglobin. Hemoglobin is a protein in your blood that carries oxygen from your lungs to your tissues and an increase in hemoglobin in your blood helps your body maintain oxygen in your bloodstream. In this example, the concentration of hemoglobin in your blood is the phenotype that changes in response to the environmental stressor of reduced oxygen availability. When you hike down to lower elevations, the hemoglobin concentrations in your blood will return to normal.

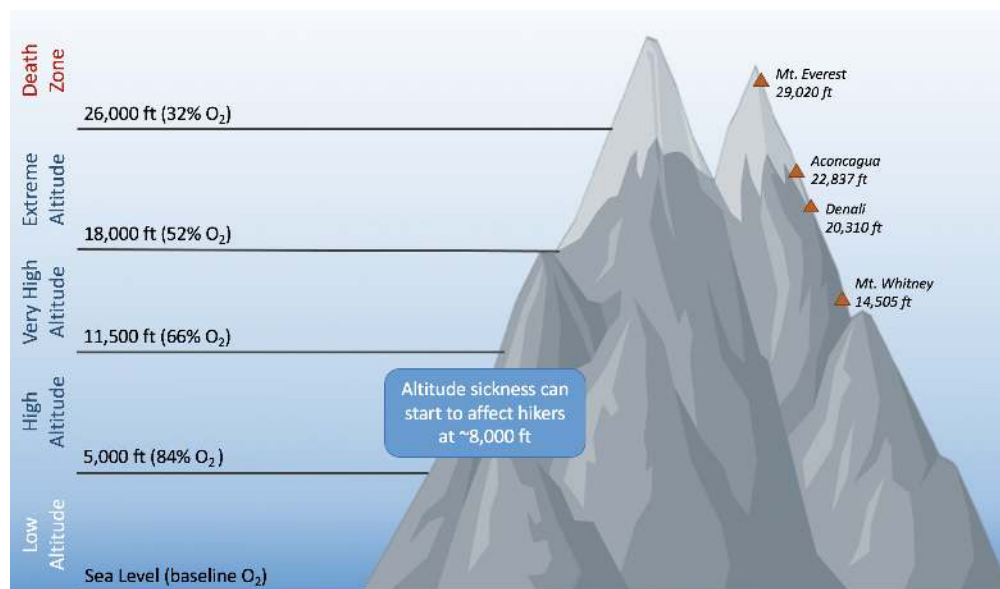


Figure 5.2.1: Diagram of the effects of altitude on oxygen availability. Considering sea level as 'baseline' (100%), reductions in O₂ levels are shown for the boundaries between low altitude, high altitude, very high altitude, extreme altitude, and the death zone (above which, human life cannot be sustained for long periods). For reference, the altitude of the tallest three mountains in the world (Everest, Aconcagua, and Denali) are provided, as well as the tallest mountain in California (Whitney). Image by L Gerhart Barley with biorender.com

Now consider the long-term impacts on a population of humans that live at very high elevations for many generations. The Tibetan Plateau, for example, has an average elevation of approximately 14,800 feet (~4500 meters) and has been inhabited by humans for possibly as long as 30,000 years. Genetic comparisons performed by [Yi et al \(2010\)](#) between Tibetan Plateau populations and their close relatives, the Han Chinese revealed differences between these groups in the frequency of different alleles for a gene called *EPAS1*. At this gene, both populations contained a particular allele that increases the production of cells called erythrocytes (which contain hemoglobin) in the blood; however, this allele was 78% more common in the high-elevation Tibetan population. In this case, differences in the frequency of *EPAS1* alleles between these two populations represent an adaptation to long-term exposure to the environmental stressor of reduced oxygen availability. We will discuss alleles and their frequencies in different populations of organisms more in the inheritance sections.

In the following sections, we will discuss acclimational and adaptational responses to abiotic (temperature) and biotic (predator/prey interactions) stressors.

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5.3: Stress - Thermoregulation

Thermoregulation (managing body temperature) is a critical consideration for all organisms due to the impact that changing temperatures have on biochemical structures and processes. For example, the rate at which many biochemical reactions (such as metabolism and photosynthesis) occur is influenced by temperature. In addition, temperature affects the shape, and therefore the functionality, of many enzymes and proteins. In fact, high temperatures can cause a protein or enzyme to denature, a process where the protein's shape is so altered that it cannot function correctly. Consequently, the metabolic processes and proteins on which an organism relies will directly influence its thermal tolerance range and so, organisms have adaptational and acclimational strategies to deal with thermal stress.

Both plants and animals exhibit acclimation to thermal stressors, whereby exposure to sub-optimal temperatures is less detrimental if the individual has prior experience under these conditions. For example, photosynthetic rate in plants is affected by air temperature and plants grown in cool conditions will exhibit maximum photosynthetic rates at lower temperatures than plants grown under warmer conditions. The same has been shown for swimming speed in fish, where fish raised in cooler water are able to maintain faster swimming speeds in cold water than fish raised in warm water. These examples show a change in the phenotype of the organisms (photosynthetic rate or swimming speed) in response to the environmental stressor of low temperature.

Animals exhibit two primary strategies in thermoregulation: ectothermy and endothermy. **Endothermic** animals rely on metabolic processes to maintain a relatively constant internal body temperature. Mammals (including humans) and birds are examples of endotherms. **Ectothermic** animals rely on the surrounding environment to regulate their internal temperature. Insects, fish, amphibians, and non-avian reptiles (such as snakes and lizards) are ectotherms. Ectothermy and endothermy should not be viewed as clear and distinct categories. Some animals, such as sharks, are primarily ectothermic, but do generate some metabolic heat when their body temperature drops below a certain threshold. Similarly, some endothermic animals do not maintain body heat while hibernating. Such animals may be termed heterotherms (switching between ectothermy and endothermy) or mesotherms (relying somewhat equally on both external and internal sources of heat). Consequently, thermoregulatory strategies should be considered as a continuum with ectothermy and endothermy as extremes. Organisms may occur anywhere along the continuum and may even move across the continuum depending on environmental conditions.

A Common Misconception

Since ectotherms rely on the surrounding environment to regulate their body temperature, it is a common assumption that an ectotherm's body temperature will follow the air temperature of the surrounding habitat. This misconception is exacerbated by figures such as the one below, which are commonly found online, and indicate that the body temperature of ectotherms directly tracks environmental temperature. This is incorrect for two reasons. First, the surrounding habitat does not exhibit a single temperature. Instead, temperature varies between sunny and shady locations, and between above- and below-ground locations, etc. Second, ectotherms do regulate their body temperature behaviorally by moving between warmer and cooler parts of the habitat, meaning that their body temperature does not necessarily track the average air temperature of the habitat.

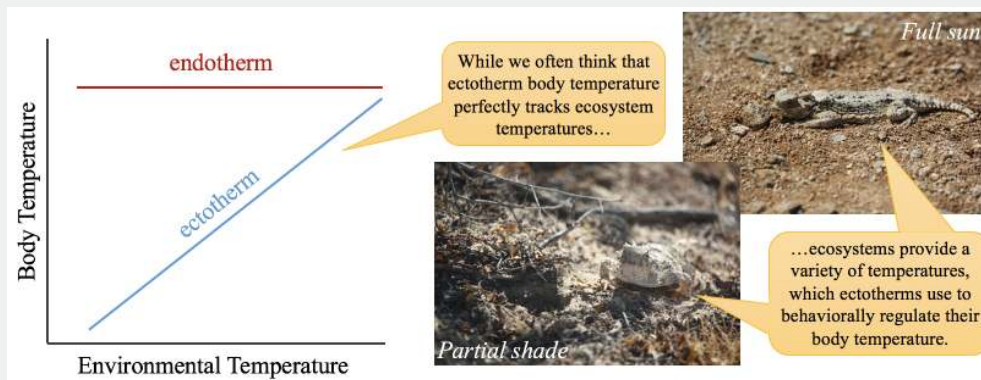


Image and photos by L Gerhart-Barley

Both animals and plants have a variety of adaptations for retaining heat in cool environments. For example, many reptiles can alter the pigmentation of their skin and will darken their body color when basking in the sun in order to increase the heating of their body. To retain heat, many animals in cold ecosystems such as polar regions are large in size, which reduces the surface-area-to-volume ratio, reducing the amount of body heat lost to the atmosphere. Similarly, animals may also have thick layers of fat (such as blubber in whales and dolphins) or fur (such as polar bears) to reduce body heat loss to the surrounding air or water. Plants have similar growth adaptations for reducing heat loss, including short growth forms to reduce heat loss from wind, and dark, horizontal leaves to increase heat uptake from the sun.

Many adaptations for increasing heat loss in warm environments take advantage of evaporative cooling. Water has a very high specific heat, meaning that it requires a high amount of energy to increase in temperature and a high amount of energy to change phases from liquid to gas. Consequently, as water evaporates from a surface it cools the temperature of that surface. Humans (and some other mammals) take advantage of evaporative cooling through sweat. Dogs cool themselves by panting. Even plants use evaporative cooling by opening pores in the leaves (called stomata) from which water evaporates and cools the plant.

Many thermoregulatory strategies result in trade-offs. For instance, reliance on evaporative cooling produces a very serious trade-off between thermoregulation and hydration where temperature stress is managed at the expense of water stress. In addition, endothermy is energetically very expensive and endotherms invest a large amount of their overall energy budget in body temperature regulation. Ectotherms avoid this energetic cost, but often spend much of their time outside their optimum temperature range, and are more at risk of entering their zones of intolerance.

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5.4: Enemies - Predation

At its simplest, we can consider predation (or herbivory) to be a function of predators (or herbivores) detecting, capturing, and consuming prey (or plant) individuals:

$$P(\text{predation}) = P(\text{detection}) \times P(\text{capture}) \times P(\text{consumption}) \quad (5.4.1)$$

where $P()$ is the probability of each factor occurring. Consequently, predators/herbivores have many adaptations for increasing these terms and prey/plants have many adaptations for decreasing them. For example, predators may increase detection through enhanced senses, such as the exceptional eyesight of raptors, while prey may decrease detection through camouflage. Predators may increase capture through strategies like pack hunting in wolves, while prey may decrease capture through defensive armor or spines. Snakes are able to unhinge their jaws in order to increase the consumption of very large prey items, while some plant leaves contain compounds such as tannins that are very difficult to digest, decreasing herbivores' consumption ability and deterring herbivory.

All of the adaptations described in the paragraph above result in trade-offs. Energy and other resources invested by prey in defensive structures or toxic compounds cannot then be put towards growth and reproduction. For predators, strategies such as pack hunting may increase the likelihood of successful capture, but also means that consumption is shared across numerous individuals.

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CHAPTER OVERVIEW

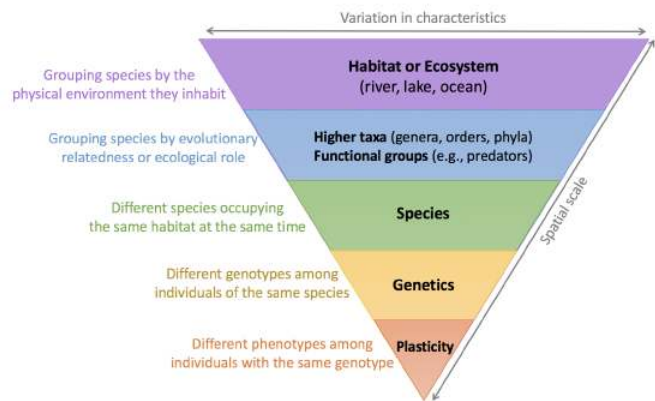
6: Functional Diversity - Life History Traits

Scientists have estimated that there are ~8.7 million species on Earth. How does one planet support such enormous diversity of species? The answer relates to the impressive functional diversity (Fig 6.0.1) that organisms display – that is, the diversity in strategies and adaptations that different organisms have for surviving in their environment. The functional diversity sections address different strategies and adaptations for acquiring nutrients and resources from the environment, dealing with stressful environmental conditions (ex. heat stress), succeeding at or defending against predation, and successfully completing the life cycle.

This chapter focuses on life history strategies and adaptations that plants and animals exhibit, and the trade offs that different life history traits confer.

Figure 6.1: Schematic of the magnitude and type of diversity exhibited at different scales. This section focuses on functional group diversity. Figure by L Gerhart-Barley.

Title Image Credit: Pennsylvania Department of Conservation and Natural Resources - Forestry, Bugwood.org; <https://www.insectimages.org/browse/...imgnum=5018091>



Topic hierarchy

- [6.1 What are life history traits?](#)
- [6.2 Trade-Offs in Life History Traits](#)
- [6.3 Patterns in Life History Traits](#)

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6.1 What are life history traits?

A species' life history is the pattern of life cycle processes, including growth, development, reproduction, and death. Life history traits, therefore, are traits that relate to the timing and occurrence of each of these stages. Such traits include the number of offspring produced per mating, the seasonal timing of mating, the age at which individuals become sexually mature, at which stage(s) individuals disperse to new ecosystems, and the average life span of an individual, among others. The principle of allocation acts on all of these traits individually, and in complex interactions, producing trade-offs that may even act across different life history stages.

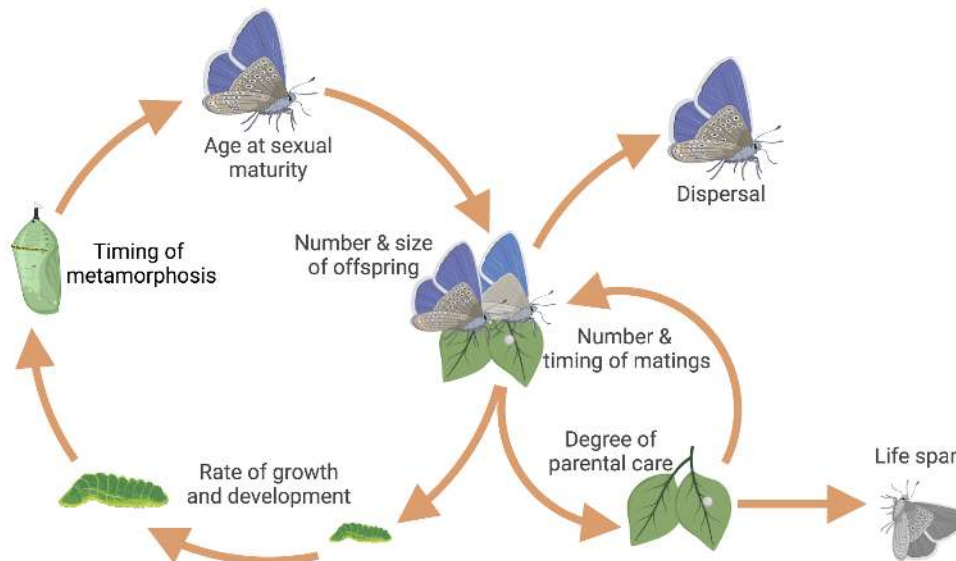


Figure 1: Life cycle diagram illustrating life history traits. (Figure by L Gerhart Barley with biorender.com)

Each stage of the life cycle in Figure 6.1.1 is labeled with some of the major life history traits associated with that stage. While the specifics of each trait will vary between individuals, each species has a particular pattern of traits. For example, in the common blue butterfly, *Polyommatus icarus*, shown in Figure 6.1.1, females usually lay a single egg per host plant. A caterpillar emerges about a week after the egg is laid and then undergoes five stages of development, called *instars*, which in total take around 7 weeks. Each instar is distinct in size and coloration, with the final instar approximately 13 mm in length. The caterpillar then forms a chrysalis, and metamorphosis into an adult butterfly takes approximately 2 weeks. The sexually mature adult butterfly has a wingspan of 2.9-3.6 cm, and lives about 3 weeks, for a total life span of about 13 weeks. Like many butterflies, and indeed many insects, adults reproduce only once and then die soon after. Consequently, the only parental care provided to the offspring are resources contained within the egg, which are about 0.6 mm in diameter. Dispersal primarily occurs during the adult stage (which is much more mobile than the caterpillar), though unlike some butterfly species, *P. icarus* is not migratory.

Semelparity versus Iteroparity

Production of offspring is a critical component of the life cycle of all organisms. Not only does reproduction contribute to the perpetuation of the species, but also the relative offspring production of individuals within a species has serious consequences for evolution and natural selection. It may be surprising, therefore, that some species reproduce only once before death, a trait called **semelparity**. Other species are **iteroparous**, meaning they reproduce many times before they die. Note that an individual of an iteroparous species who reproduces only once and then dies by accident would not be considered semelparous; instead, semelparity is a trait by which all or the vast majority of individuals invest all of their resources in a single reproductive event, which results in their death.

One example of a semelparous species is the 17-year periodical cicada, *Magicicada septendecim*, shown in Figure 6.1.2. This species spends 17 years in underground burrows (Fig. 6.1.2A), before emerging as a sexually immature juvenile stage called a nymph (Fig. 6.1.2B). Within days, the nymphs will molt into sexually mature adult cicadas (Fig. 6.1.2C) and mate (Fig. 6.1.2D).

After mating, the female lays her eggs on tree branches; in Fig. 6.1.2E, each slot on the tree branch behind the female contains a single egg. The adult stage of the life cycle lasts only a few weeks; after mating and egg laying, the adults die. The eggs the females have laid will hatch after about 6-10 weeks, and the resulting nymph (Fig. 6.1.2F) will migrate out of the tree and burrow into the ground, where it will grow and develop, re-emerging 17 years later.



Figure 2: Stages of the 17-year periodical cicada life cycle. A) the underground burrows from which late-instar nymphs emerge; B) a late-instar nymph; C) a freshly molted, sexually mature adult; D) cicadas mating; E) a female cicada laying eggs on a tree branch; F) an early-instar nymph, recently hatched from its egg. (Images from Wikimedia Commons, Pennsylvania Department of Conservation and Natural Resources, and Maryland Department of Agriculture¹⁻⁶)

Under what conditions would only one reproductive event be beneficial? If high numbers of offspring are important for the survival of the species and for an individual's evolutionary fitness (both of which are true), then wouldn't it always be beneficial to reproduce many times? In what cases would it actually increase the individual's fitness (total number of offspring produced during its life) to invest all its resources in the first reproductive event and save none for its own survival or growth? We can answer these questions by studying species that exhibit semelparity.

Research on semelparous species has shown that individuals produce far more offspring per reproductive event than their iteroparous relatives, presumably due to the investment of all available resources into offspring (rather than saving some resources for survival of the individual). However, the question still remains: how much more offspring must a single reproductive event produce in order to outweigh the additional offspring gained from later reproductive events? The answer lies in the likelihood of later reproductive events. Semelparity becomes beneficial if the probability of an individual surviving long enough to reproduce again is very low. Consequently, in harsh, unstable, or unpredictable environments, semelparity ensures the highest number of offspring out of the only reproductive event the individual is likely to experience. In environments that are more stable, predictable, and conducive to survival, iteroparity is likely to result in the highest number of offspring.

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6.2 Trade-Offs in Life History Traits

The **Principle of Allocation** states that an organism has a finite (or limited) quantity of resources (energy, nutrients, etc) to invest in the various processes that sustain life. Resources that an organism invests in one process cannot also be invested in other processes, which produces trade offs in the decisions organisms make about resource investment. This section will discuss some of the major trade offs associated with various life history traits and strategies and how these trade offs produce sets of traits that are commonly found together.

As outlined in the previous section, a fundamental life history trait is the number of offspring produced per mating. This number varies widely across organisms. Bison (*Bison bison*) and other large mammals produce an average of one offspring per mating, as illustrated in Fig 6.2.1A where each female escorts a single calf. Other organisms produce many offspring at a time, such as the European grass frog (*Rana temporaria*, Fig 6.2.1B) which can lay up to 2,000 eggs in a single reproductive event (Fig 6.2.1C).



Figure 1: A) Female bison (*Bison bison*) and calves. B) Female European grass frog (*Rana temporaria*). C) *Rana temporaria* egg mass containing as many as 2,000 eggs from one mating. (Images from Wikimedia Commons¹⁻³)

A critical trade-off in offspring number relates to the relative size of the offspring. Generally, an individual has a finite amount of resources to invest in producing offspring, which means that a larger number of offspring will be, on average, smaller in size than if only few offspring were produced. This pattern is seen both within and across species. For example, when comparing plant species in the family *Asteraceae*, species that produce relatively larger seeds also produce fewer seeds per reproductive event, while species that produce relatively small seeds also produce more seeds per reproductive event. Even within a species, individuals who produce more offspring per reproductive event will, on average, produce smaller offspring. Consider, for example, the size and number of human offspring. Though multiple births (twins and triplets) do occasionally occur naturally, humans generally produce a single offspring per mating and at birth, single-birth babies weigh on average ~7.5 pounds (3.5 kg). Twins, however, weigh on average ~5.5 pounds (2.5 kg) and triplets ~4 pounds (1.8 kg). With advances in medical technology such as in-vitro fertilization, it is possible for women today to carry many more offspring than would normally occur. Famous examples of sextuplets and octuplets have occurred in recent years, which follow the expected pattern of birth weight and number. Kate Gosselin's sextuplets born in 2004 weighed on average 2.7 pounds (1.2 kg) at birth and Nadya Suleman's octuplets born in 2009 weighed on average 2.5 pounds (1.11 kg) at birth. In species like humans where offspring are carried inside the parent's body as they develop, the trade-off in number and size of offspring is not just about energetic or nutritional resources, but also about space. Even with medical advances in fertilization techniques, the human body can only hold so many babies.

The trade-off between offspring size and number influences the survival of offspring as they mature. This is an example of trade-offs that occur across life cycle stages, meaning that the benefits and costs to a particular decision are experienced by the organism

at different stages in the life cycle. For example, consider the plants in the *Asteraceae* family mentioned in the previous paragraph. Larger seeds contain more nutritional content for the developing embryo plant. Consequently, species that produce larger seeds will likely have higher seed and seedling survival, as the juvenile plant has more resources available early in development. If small seeds are less likely to survive to seedlings, why would any plant species produce small seeds? First, recall that smaller seeds are also more numerous, and so, even though the likelihood of any one seed surviving is lower, there are more total seeds, and so more 'chances' for offspring to survive the juvenile stage. Second, in these species, smaller seeds have a different advantage over large seeds: dispersal. Smaller seeds are better able to travel on the wind than larger (and heavier) seeds, and so have an advantage at a different life history trait than large seeds. Large seeds may have another advantage, however: competition. With their higher nutritional resources, large seeds are more likely to successfully compete with other plants, especially at the juvenile stage when the seedlings primarily rely on nutritional resources within the seed before being able to fully access resources from the air and ground.

The descriptions above illustrate the complexities of trade-offs in life history traits both within and across life cycle stages. The initial trade-off between seed number and seed size leads to different benefits or drawbacks in future life history traits such as seed dispersal, seedling survival, and seedling competitive success. Large seeds exhibit a higher likelihood of survival and stronger competitive advantage, but are few in number and unable to disperse long distances. Small seeds are numerous and able to disperse further than large seeds, but are less likely to survive as seedlings and struggle more in competition with other species.

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6.3 Patterns in Life History Traits

The types of trade-offs illustrated in the previous section result in many species exhibiting particular groupings of life history traits that have complementary trade-offs. In this section, we will consider two examples of these groupings, ***r*-selected species** and ***K*-selected species**. The terms *r* and *K* are components of the population growth equation, which is discussed in detail in the Population Growth and Dynamics section. Table 6.3.1 shows traits, characteristics, and representative examples of species that are highly *r*-selected and species that are highly *K*-selected. These two categories represent two ends of a continuum, and so not all species are considered either *r*-selected or *K*-selected; instead some species (as we will discuss below) may fall in the middle of the continuum (and be neither *r*-selected nor *K*-selected) or have traits at each of the continuum (and so, in a sense be both *r*-selected and *K*-selected).

Trait	<i>r</i> -Selected	<i>K</i> -Selected
Habitat	Generalists and able to tolerate unpredictable or variable environments; poor competitors	May be specialists; strong competitors in stable, predictable environments
Reproductive Traits	Produce many small offspring; limited if any parental care of offspring; often semelparous	Produce few large offspring; high parental investment in offspring success; often iteroparous
Adult Traits	Small body size; short life span; early reproductive maturity	Large body size; long life span; late reproductive maturity
Population Demographics	Highest mortality in juvenile life stages (Type III curve); density-independent drivers of population size; prone to "boom and bust" population cycles controlled by intrinsic rate of increase (<i>r</i>)	Highest mortality in late adult stages (Type I curve); density-dependent drivers of population size; relatively stable population size controlled by carrying capacity (<i>K</i>)
Representative Species		

Table 1: Traits and characteristics of *r*-selected species and *K*-selected species. (Images from Wikimedia Commons¹⁻⁶)

Recall the trade-off related to offspring size and number. We discussed that a larger individual offspring has a higher likelihood of succeeding, but that more numerous (and therefore smaller) offspring represent more 'chances' at successful maturation. Offspring size (especially in traits such as egg or seed size) directly relates to parental investment in offspring, though parental investment can also involve care as the offspring matures. Consider the bison (*Bison bison*) and European grass frog (*Rana temporaria*) discussed previously, and included again below. A female bison may produce one (or, rarely, two) calves in each annual reproductive event. The female carries the offspring within its own body, nourishing and protecting it, for a gestation period of ~283 days. Calves are nourished solely by milk produced by the female bison for approximately 7 months, and even after weaning remain near their mother for protection and care for an additional five months. Because of this care and support, a large proportion of calves born in a given year generally survive to maturity. Conversely, a female *Rana temporaria*, lays up to 2,000 eggs per reproductive event and clusters them together in a mass (Figure 6.3.1C), which she does not tend or protect or nourish. The only parental care provided by the female in this case, is the nourishment contained within the egg when it is laid. Consequently, the eggs are vulnerable to predators, pathogens, and environmental stressors (such as the pool drying out) and experience a high degree of mortality before hatching into tadpoles. These two species illustrate the differences in reproductive strategies between *r*-selected (*Rana temporaria*) and *K*-selected (*Bison bison*) species.



Figure 1: A) Female bison (*Bison bison*) and calves. B) Female European grass frog (*Rana temporaria*). C) *Rana temporaria* egg mass containing as many as 2,000 eggs from one mating. (Images from Wikimedia Commons⁷⁻⁹).

They differences in offspring number and size and degree of parental care result in different survival patterns throughout the developmental stages of individuals. Species with Type I survivorship curves have high offspring survival and a large proportion of individuals survive to adulthood and reproductive maturity. The highest degree of mortality occurs in advanced adult age groups. Type I survivorship curves are therefore characteristic of K-selected species. Type III survivorship curves exhibit significant juvenile mortality such that the majority of offspring never reach sexual maturity. Type III survivorship curves are characteristic of r-selected species. Type II survivorship curves exhibit relatively constant survivorship and mortality throughout different age groups and therefore are not r-selected or K-selected, but instead somewhat in the middle of the continuum between the two.

As the types of survivorship curves illustrate, r-selection and K-selection exist on a continuum, not as discrete groupings. Some organisms are somewhat in the middle. For example, many medium-sized mammals and birds might fall in this area. Organisms in the middle of the continuum are neither quite large nor small, have middling life spans and rates of growth, produce moderate numbers offspring in which they invest a moderate amount of resources and parental care. Many also exhibit a Type II survivorship curve.

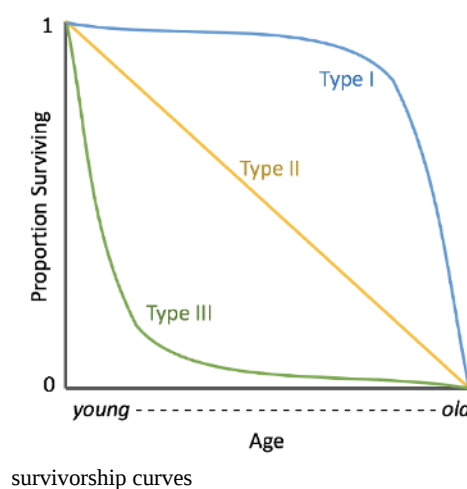


Figure 2: Example of Type I, II, and III survivorship curves

Additionally, other organisms seem to exist at both ends of the continuum, exhibiting some highly r-selected traits, and other highly K-selected traits. For example, leatherback sea turtles (Fig 6.3.3) are among the largest and longest-lived reptiles, with average

weight in excess of 1,000 pounds (454 kg) and average life spans estimated at 50-100 years, both of which would indicate *K*-selection. In reproduction, however, female leatherbacks lay around 110 eggs, do not tend or protect the nest and do not return to care for nestlings once they hatch. The small size of hatchlings makes them highly vulnerable to predation until they reach a sufficiently safe size, producing a Type III survivorship curve. These traits indicate *r*-selection. Species such as leatherback sea turtles are therefore difficult to categorize on the *r* to *K* continuum.

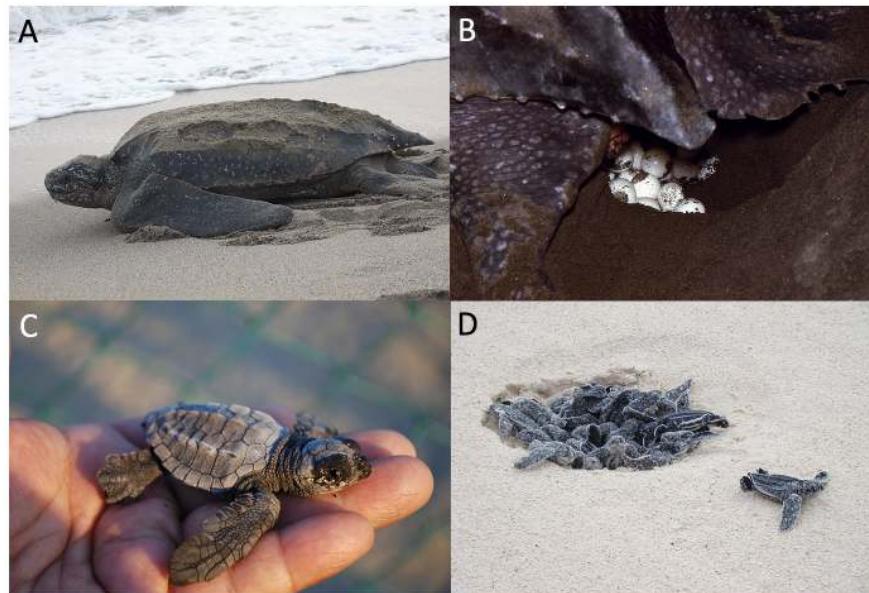


Figure 3: A) adult leatherback sea turtle; B) female leatherback laying eggs; C) recently hatched juvenile leatherback (in human hand for scale); D) juvenile leatherbacks emerging from the nest. (Images from Wikimedia Commons¹⁰⁻¹³)

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CHAPTER OVERVIEW

7: Population Growth and Dynamics

Recall that one of the scales of ecology is **populations**, or groups of individuals operating in the same time and place (Fig 7.0.1). Important considerations for populations include the number of individuals in the population, termed **population size**, and the patterns and drivers of changes in the population size across space and time, termed **population dynamics**. These concepts consider how the life history traits discussed in the previous section such as reproductive output, dispersal, and life span of individual organisms scale up to population growth or decline across space and time.



Figure 7.1: Examples of scale in ecological research. (UC Davis Arboretum photos by L Gerhart-Barley, Earth image from Wikimedia Commons¹)

7.1: Exponential Growth

7.2: Controls on Population Growth

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Title Image: photo by L Gerhart-Barley

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7.1: Exponential Growth

At its simplest, changes in population size are determined by the relative balance of new members joining the population and current members leaving the population. For instance, new members may join the population through birth of new offspring or by immigration from other nearby populations of the species. Similarly, current members may leave the population through death or via emigration to other nearby populations. These processes can be represented mathematically:

$$N_t = N_0 + B - D + I - E \quad (7.1.1)$$

where N_t is the size of the population at a time in the future, which is the result of the current population size N_0 , and the number of individual births (B), deaths (D), immigrants (I), and emigrants (E) that occur in that time interval. To estimate the population growth rate (the speed at which the population size changes through time), we can rewrite the previous equation as

$$\Delta N = B - D + I - E \quad (7.1.2)$$

where ΔN represents the change in population size from time 0 to time t. If we consider a 'closed' population with no connection to other nearby populations, we can assume no change in population size from immigration or emigration, reducing our equation to

$$\Delta N = B - D \quad (7.1.3)$$

Since the number of births and deaths that occur depend on the size of the population and the time length considered, it is important to convert numbers of births and deaths in the population into rates; the average number of births per individual per unit time (the per capita birth rate, b), and the average number of deaths per individual per unit time (the per capita death rate, d). These changes result in the following equation

$$\Delta N = (b-d) N_0 \quad (7.1.4)$$

where N_0 is the population size at time 0. We can then summarize the per capita birth and death rates as the overall per capita growth rate r, which is the difference between the per capita birth and death rates. This change reduces the equation to

$$\Delta N = r N_0 \quad (7.1.5)$$

This equation represents the change in a population's size through time given the balance between its birth and death rates. If birth rates are higher than death rates ($b > d$) then $r > 1$ and the population size will increase through time ($N_t > N_0$). If birth rates are lower than death rates, ($d > b$) then $r < 1$ and the population size will decrease through time ($N_t < N_0$). If birth and death rates are equal, ($b = d$) then $r = 1$ and the population size will remain constant through time ($N_t = N_0$). Figure 7.1.1 illustrates these possible outcomes.

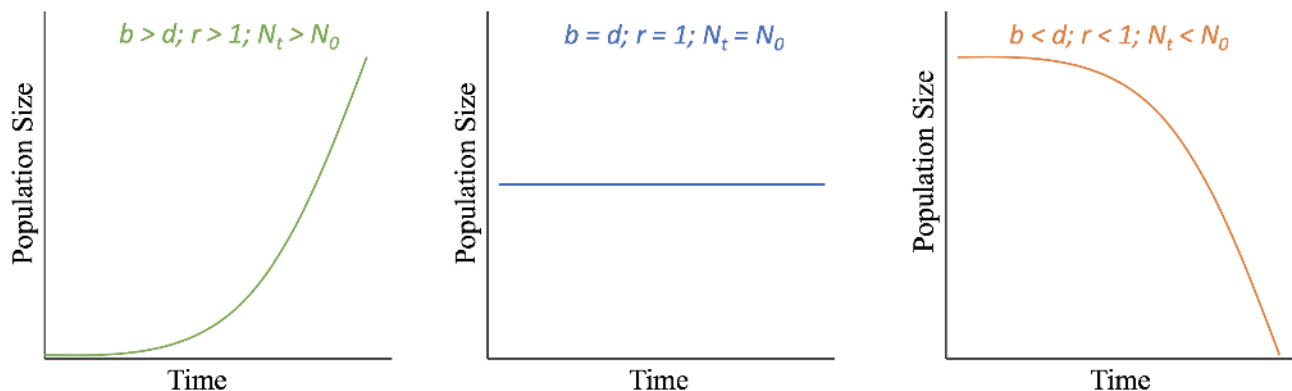


Figure 7.1.1: Illustrations of how the balance between birth rates (b) and death rates (d) affect population growth rates (r) and the population size through time. (Figures by L Gerhart-Barley.)

Using calculus, we can adjust the equation to represent very short, nearly instantaneous periods of time, which allow us to represent population growth as a curve instead of as discrete points along a line.

$$dN/dt = r N_0 \quad (7.1.6)$$

Equation 7.1.6 allows us to predict the change in the size of a population across time, but it does not allow us to predict the actual population size at the end of that time period. In other words, we could estimate how many individuals might be added to or lost

from the population, but not what the final number would be. Using calculus, we can integrate Equation 7.1.5 to an equation that does allow us to estimate future population size:

$$N_t = N_0 e^{rt} \quad (7.1.7)$$

where e is a constant, the base of the natural log ($e = 2.718$) and t is the time interval between time 0 and time t . Knowing the current population size (N_0) and the per capita growth rate (r), we can then estimate the population size at future time t , which we call N_t .

This growth pattern is termed exponential growth because it results in the curvilinear growth trends illustrated in Fig 7.1.1, where large increases in the population occur as the population (N_0) increases. The pattern of increase also relates to the growth rate, r . When r is positive, higher r values will result in faster increases in population size than lower r values (Fig 7.1.2). When r is negative, lower (more negative) values of r lead to faster population decline. Consequently, the pattern of growth a population experiences is a result of both its current population size and its per capita growth rate.

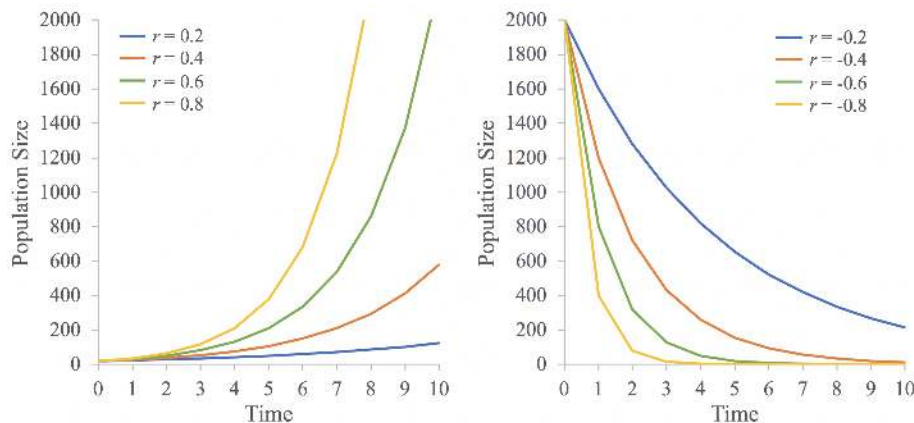


Figure 7.1.2: The influence of different values of r on population size through time. (Figure by L Gerhart-Barley)

Exponential Growth in Natural Populations

Some naturally-occurring populations exhibit exponential growth patterns. For example, pollen studies of sediment in Hockham Mere bog in Norfolk County, England spanning the last 10,000 show exponential growth in many tree species (Fig 7.1.3). These species expanded into Hockham Mere as glaciers retreated from the region, exposing new land area. While the details of the population growth patterns vary between the species, each shows the characteristic exponential pattern of initial slow growth when the population size is small, and more rapid growth as the population size increases.

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Figure 7.1.3: Examples of exponential growth in populations of several tree genera surrounding Hockham Mere in Norfolk County, England following the retreat of glaciers from the area (Figure taken from [Bennett et al 1983](#))

Exponential decline also occurs in populations. In some cases, this can be beneficial. For instance, viruses such as Hepatitis C and COVID-19, cannot survive indefinitely outside of a host. Consequently, viral populations infecting exposed surfaces experience exponential decline, reducing the risk of transmission of the viral infection over time. In other systems, however, such as the case of threatened and endangered species, exponential decline is of serious concern. For example, some loggerhead sea turtle

populations in Japan and Australia have exhibited exponential decline in response to increasing sea surface temperatures caused by anthropogenic climate change (Fig 7.1.4).

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Figure 7.1.4: Population sizes through time of four loggerhead sea turtle populations (a-d, right) and a map of the location of these populations (left). Figures from [Chaloupka et al 2008](#).

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7.2: Controls on Population Growth

The exponential growth model assumes that all offspring survive to reproductive maturity and produce offspring themselves. We know that this assumption does not hold true in many naturally-occurring populations. For instance, the life history section highlighted that high juvenile mortality is a characteristic trait of r-selected species. What factors influence these rates of mortality, and exert what scientists call ‘controls’ on population growth? Scientists generally categorize controls on population growth into two groups: density independent controls and density dependent controls.

Density independent controls are factors that do not depend on how large the population is (ie. its density); the number of individuals currently present in the population does not influence the likelihood of an individual to die from density independent factors. Generally, though not always, density independent controls are **abiotic factors**. For example, in December of 2006 a severe ice storm hit much of the Midwest. In Nebraska, tree branches were coated with as much as 1.5 inches of ice (Figure 7.2.1). Many trees could not bear the enormous weight of so much ice. Nearly all trees lost branches, and many simply collapsed entirely. Whether or not an individual tree could withstand the weight of the ice was not influenced by the density of other trees in the area. A given tree either could, or could not, support the weight of the ice on its branches. A given tree’s survival during the ice storm was, therefore, independent of the density of other trees in the area.



Figure 7.2.1: Ice coats a tree branch in Nebraska after an ice storm in December 2006. (Photo by John Love, courtesy of the [National Weather Service](#))

Density dependent controls are factors that do depend how large the population is (ie. its density); the number of individuals present in the population does influence the likelihood of an individual to die from density dependent factors. Generally, though not always, density dependent controls are biotic factors. For example, pathogens and parasites are more easily transmitted between individuals when densities are high. Similarly, resources such as space, food, and nutrients become relatively less available as the population size that relies on them increases (Figure 7.2.2). Consequently, an individual organism’s likelihood of being impacted by these factors increases as the population density increases.



Figure 7.2.2: Resources such as space are density dependent. Their influence on the population changes as density of the population changes. (Photo by David Stanley)

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