Biogeography: a brief introduction

Kenneth W. McCravy

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KENNETH W. MCCRAVY

BIOGEOGRAPHY: A BRIEF INTRODUCTION

Biogeography: a brief introduction
1st edition

ISBN 978-87-403-1332-1
Peer review: Shawn Meagher, Ph.D., Department of Biological Sciences,
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1 WHAT IS BIOGEOGRAPHY?

Your goals for this chapter are to learn about:

- The kinds of questions that biogeographers ask
- The interdisciplinary nature of biogeography

Why are polar bears found in the Arctic, but not the Antarctic? How do ground beetles end up on isolated oceanic islands? Why is the flora and fauna of Australia so unique? How did humans make it to the New World, and what was their impact on other forms of life there? Questions about the distribution of life on Earth have been asked since the time of Aristotle and before. Seeking answers to these questions is the province of the science of **biogeography** – the study of spatial and temporal patterns of biological diversity, or biodiversity. Biodiversity is the variation present in the biological world, and this term can refer to variation at different scales: genetic, population, species, community, and ecosystem.

At the most fundamental level, biogeography seeks to inventory the plants and animals of particular geographic locations and ecological habitats. Such basic information can be critically important in, for instance, assessing the changes in biodiversity that result from such causes as habitat fragmentation or climate change. But the more interesting questions tend to be the "how?" and especially the "why?" questions such as the ones listed above. Traditionally, questions that biogeographers ask are divided into two categories, historical biogeography and ecological biogeography. **Historical biogeography**, as the term suggests, focuses on long term processes that unfold over evolutionary or geological time periods, and often involves large scale geographic areas and taxa that are extinct. **Ecological biogeography**, on the other hand, generally deals with shorter time periods, smaller geographic scales, and extant taxa. Study of the effects of plate tectonics on the distribution of dinosaur fossils is an example of historical biogeography; investigation of the relationship between tropical mountain elevation and species diversity of butterflies would fall under the purview of ecological biogeography. Biogeography is also often subdivided into **phytogeography** (the study of plant distributions) and **zoogeography** (the study of animal distributions). But of course the biogeography of plants and animals is highly intertwined, so it is difficult if not impossible to study one group without substantial reference to the other.

Biogeography is a highly integrative science. As is apparent from the name, at the basic level biogeography is a synthesis of biology and geography. But biogeography integrates knowledge from many different fields. Biogeography goes hand-in-hand with evolutionary biology and systematics; the role of geographic isolation is a central one in evolution, as observed by, among others, Charles Darwin almost two centuries ago. Genetics plays an essential role here of course; isolation leads to and maintains genetic differentiation and speciation. Ecology, physiology and climatology are also important in biogeography. The distributions of organisms are constrained to a great degree by factors such as presence of predators and parasites, competition for food and other resources, and the organism's own physiological abilities to survive and reproduce in particular climatic conditions. Unraveling of past distributions of organisms depends to a great extent on the study of fossil forms – paleontology. As a matter of fact, the importance of fossils in our biogeographical understanding has led to the new sub-discipline of **paleobiogeography**. Finally, the science of geology has contributed enormously to our understanding of the forces that shape biogeographical patterns. As Dennis McCarthy points out in his book *Here Be Dragons: How the Study of Animal and Plant Distributions Revolutionized Our Views of Life and Earth*, biogeography really represents a unification of the fundamental theories of two natural sciences, the theory of evolution by natural selection (biology) and the theory of plate tectonics (geology).

In addition, biogeography is highly relevant to more applied fields such as conservation biology and human ecology. Habitat destruction and the spread and establishment of invasive species are major threats to biodiversity that are strongly intertwined with biogeography, and evidence suggests that animal and plant distributions are already being influenced by anthropogenic climate change. A thorough understanding of biogeographical principles will be required to understand and successfully meet these challenges.

In the following chapters, the fundamentals of biogeography will be presented. After an overview of the history of the development of biogeography as a science, we will examine plate tectonics and evolution, the bedrock concepts of geology and biology. We will then focus on ecology and patterns of biodiversity, marine biogeography, and the biogeography of islands. An overview of biogeographical patterns over geological time periods will follow. We will then conclude with a discussion of human biogeography and the impacts of humans on the biogeography of other species. Hopefully, this book will provide an introduction to further study, and stimulate an interest in, as Charles Darwin put it in an 1845 letter to the eminent botanist Joseph Hooker, "that grand subject, that almost keystone of the laws of creation, Geographical Distribution."

1.1 REFERENCES AND FURTHER READING

Cox, CB & Moore, PD 2010, *Biogeography: an ecological and evolutionary approach*, 8th edn. John Wiley and Sons, Hoboken, New Jersey.

Lomolino, MV, Riddle, BR, Whittaker, RJ & Brown, JH 2010, *Biogeography*, 4th edn. Sinauer Associates, Sunderland, Massachusetts.

McCarthy, D 2009, *Here be dragons: how the study of animal and plant distributions revolutionized our views of life and Earth*. Oxford University Press, New York.

2 BIOGEOGRAPHY – DEVELOPMENT AND HISTORY

Your goals for this chapter are to learn about:

- How science progresses
- How biogeography is, in one sense, a young science, but in another sense an ancient science
- Linnaeus' major contributions to science
- How the Christian worldview of the 18th and 19th centuries limited progress in biogeography
- Linnaeus' "paradisical mountain" concept, and Comte de Buffon's criticisms of it
- The contributions of the major botanists to biogeography in the late 18th to early 19th centuries
- The importance of the work of Charles Lyell to evolutionary biology and biogeography
- The fundamental concepts of the theory of evolution by natural selection
- The evidence for natural selection that Darwin found while on his voyage aboard the HMS *Beagle*
- The work of Alfred Russel Wallace, who shares credit with Darwin for the theory of evolution by natural selection
- Disjunct distributions, and how late 19th century biogeographers attempted to explain these distributions
- The theory of plate tectonics, and how it provided a plausible explanation for gondwanan distributions such as that of the seed fern genus *Glossopteris*
- The major advances in biogeography in the latter half of the 20th century

2.1 INTRODUCTION

In his influential book, *The Structure of Scientific Revolutions*, the philosopher of science Thomas Kuhn suggested that scientific progress does not occur in a consistent, accumulative fashion, but rather is punctuated by periodic "paradigm shifts" in which the accepted view is, in a relatively short period of time, radically transformed. While there is disagreement among scientists and philosophers as to what constitutes a paradigm shift and how often they occur, it is clear that the view held by most non-scientists of scientific progress as a dry, orderly, stepwise process, achieved by following the scientific method in a cookbook fashion, is inaccurate. In reality, science is messier, but far more interesting than this, with many blind alleys, controversies, arguments, and conflicting data. Science is conservative by nature, in the sense that it takes overwhelming evidence to overturn an existing paradigm. This can be viewed as a self-regulating mechanism. While science and scientists must, of course, be open to consideration of new ideas, these ideas must have some evident merit to be considered seriously. As the late great astrophysicist and popular science author Carl Sagan once stated, "It pays to keep an open mind, but not so open your brains fall out." The history of the science of biogeography is a fascinating story that illustrates how science progresses, both in terms of the ideas put forth as well as the people who formulated them. Science is people-driven, and the science of biogeography has had more than its share of interesting personalities.

2.2 EARLY BIOGEOGRAPHY

Biogeography has only been recognized as a formal, distinct scientific discipline for a few decades, but humans have been studying plant and animal distributions for centuries and even millennia. It may not be too much of a stretch to think of early hunter-gatherer humans as primitive biogeographers in the sense that a working knowledge of distributional patterns of game animals and edible plants was essential to their survival. In historical times, early Greek philosophers contemplated the distributional patterns of nature; among his many other questions about the nature of things, **Aristotle** (384–322 BCE) asked how life arose and spread, and formulated an early classification of living things. Aristotle's successor, **Theophrastus** (371–287 BCE) focused on botany, and wrote voluminously on classification of plants based on a variety of characteristics, including locality. Theophrastus is sometimes referred to as the "father of botany." Although these early attempts to understand biodiversity were fraught with assertions we would consider absurd, they also included insights that were quite impressive even by today's standards.

2.3 EXPLORATION AND BIOGEOGRAPHY

Knowledge of the world's flora and fauna accelerated greatly in the 18th century during a period known as the "age of exploration." European explorers and naturalists were travelling, collecting and cataloging specimens from throughout the world. It became apparent that a system was needed to organize and classify the astounding diversity of organisms that were being discovered and collected.

About 2,000 years after Theophrastus, a man whose name would become synonymous with biological classification was born in the village of Råshult, in southern Sweden. **Carolus Linnaeus** (1707–1778) believed that God put him on Earth to devote his life to describing and cataloging the natural world (Fig. 2.1). To borrow a phrase from the 1980s movie *The Blues Brothers*, it could be said that Linnaeus considered himself to be on a "mission from God" to explain the mysteries of the "divine museum." The two achievements for which Linnaeus is most well-known (and that make him so beloved by students of biology when learning scientific names ☺) are the Linnaean classification system and the system of binomial nomenclature. The former was a hierarchical system that classified and organized living things based on their similarities; it is a system that is still used in revised form today. The latter, also still in use, is a system of naming species that includes a unique, two part (genus and specific epithet) scientific name for each species. But in addition to naming and classification, Linnaeus was also driven to explain the origin, spread, and distribution of life. Linnaeus documented his work in four major publications: *Systema Naturae*, *Species Plantarum*, *Genera Plantarum*, and *Philosophia Botanica*.

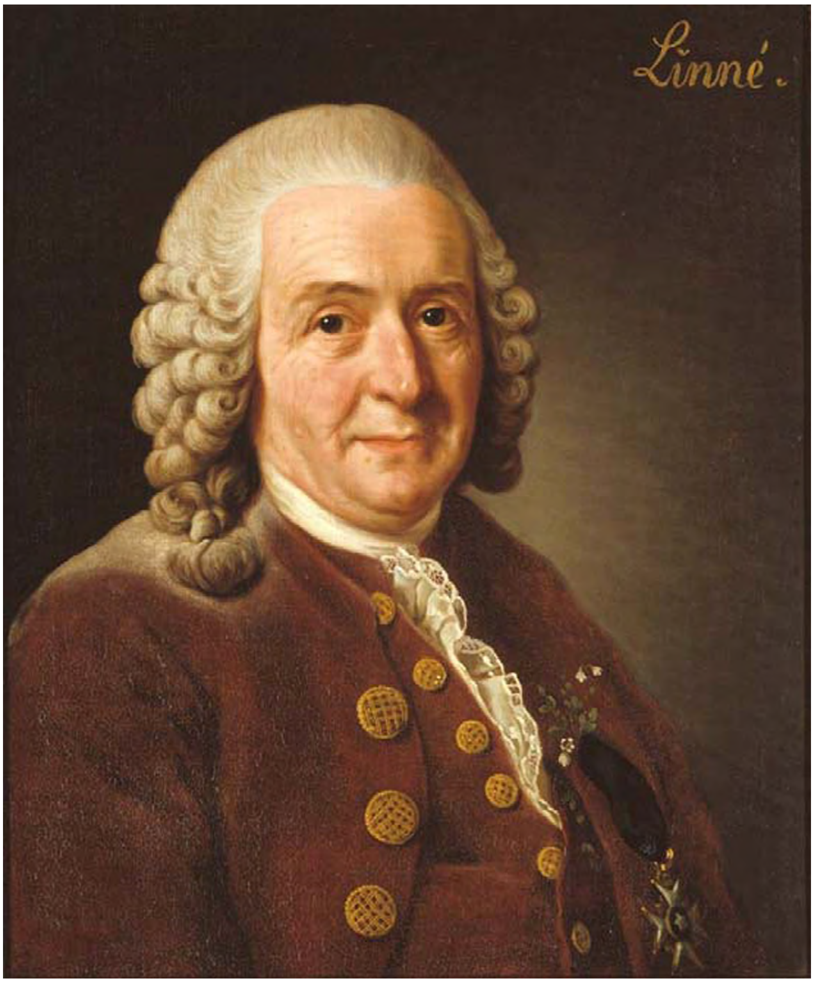


Figure 2.1: Carolus Linnaeus, the father of modern taxonomy (Wikipedia 'Carl Linnaeus;' Attribution: Nationalmuseum press photo, cropped with colors slightly adjusted; 1866: transferred to Nationalmuseum from Gripsholm Castle)

Like other naturalists of his time, Linnaeus lived within the framework of a Christian worldview, and his thinking was subject to this constraint. He believed that God created all species at one time and at a single location. Furthermore, these species, as well as the Earth and its climate, were immutable, that is, they were unchanging and could not adapt to new conditions. So how could these immutable species have come to occupy their suitable habitats throughout the world? Linnaeus proposed the existence of an equatorial "paradisical mountain," an island-mountain where creation took place. When the waters receded and the landmasses expanded, the various species dispersed to their new locations and habitats throughout the world. Because high elevation tropical mountains include different habitats, from lowland tropical forests to high altitude tundra, this paradisical mountain allowed for the creation of the different species within their appropriate habitats, so that when the species dispersed, they were well suited for their new location.

Georges-Louis Leclerc, **Comte de Buffon** (1707–1788) was a contemporary of Linnaeus and an accomplished naturalist in his own right (Fig. 2.2). He noted a couple of problems with Linnaeus' paradisical mountain hypothesis. First, Buffon noted that different regions of the world, even those with similar environmental conditions, had different species. This observation would become known as Buffon's law, and is a basic principle of biogeography. This is unlike what would be expected if each habitat of the paradisical mountain supplied species for that habitat type throughout the world. Second, if species could not adapt, then how could they survive when moving from the mountain through areas with unfavorable environmental conditions to get to their suitable habitats and locations?

Figure 2.2: Georges-Louis Leclerc, Comte de Buffon, one of the most influential naturalists of the late 18th century (Wikipedia 'Georges-Louis Leclerc, Comte de Buffon;' Attribution: Musée Buffon à Montbard)

Like Linnaeus, Buffon believed in a single creation event, but Buffon hypothesized a northern origin of life during a warm period in the Earth's climate. Then, as the climate cooled, species dispersed south, adapting to their new environments. Those species that did not adapt died out. We now know that Buffon's hypothesis, like Linnaeus', was off the mark. But Buffon's ideas provided an important advance: he recognized the dynamic nature of the Earth, its climate, and its species. Buffon also provides a good example of how science often progresses; he proposed an imperfect hypothesis, but contained within that hypothesis were valuable ideas upon which others could build.

An important explorer of the mid-to-late 18th century was Captain James Cook, who, although not a scientist, was accompanied by three accomplished naturalists of the period: Sir Joseph Banks (1743–1820), **Johann Reinhold Forster** (1729–1798), and his son Johann Georg Adam Forster (1754–1794). In particular, the elder Forster made important contributions to plant biogeography (Fig. 2.3). He verified that Buffon's law applied to plants as well as animals, recognizing that distinct plant assemblages are associated with similar environmental conditions in different regions. He also made important contributions regarding patterns of plant diversity and island biogeography, observing that plant diversity increases with decreasing latitude (i.e., approaching the equator) and that larger islands with more varied habitats tend to have greater numbers of plant species than do smaller islands.

Figure 2.3: Johann Reinhold Forster (left) and his son Johann Georg Adam Forster (Wikipedia 'Johann Reinhold Forster;' Attribution: 1775–80 painting by John Francis Rigaud)

2.4 FURTHER BOTANICAL CONTRIBUTIONS

Knowledge of phytogeography was expanding rapidly by the end of the 18th century, driven by botanists such as the elder Forster, **Karl Willdenow** (1765–1812), **Alexander von Humboldt** (1769–1859), and **Augustin de Candolle** (1778–1841). This period marked the culmination of the historical period known as the "age of enlightenment," in which reason and analysis were emphasized, and the influence of traditional authorities such as the Catholic church declined. The values of the enlightenment influenced and were reflected in the work of these naturalists. Karl Willdenow wrote a major work synthesizing knowledge of plant distributions in relation to climate. He also proposed an explanation of plant distributions based on multiple simultaneous creations in many different places rather than a single creation event. Willdenow was a friend and mentor of Alexander von Humboldt (Fig. 2.4), and introduced Humboldt to botany. Humboldt traveled extensively, particularly in the Neotropics. He wrote many important works; his *Essay on the Geography of Plants* was a major contribution to science, graphically illustrating the relationships between plants and climate. Humboldt also expanded Forster's observations on latitudinal gradients of biodiversity to include altitudinal gradients. The importance of Humboldt's insights to the field of biogeography is reflected in his recognition as the "father of phytogeography." Candolle made important contributions to knowledge of plant dispersal and the barriers to this dispersal. He studied the adaptations that plants show in response to climatic conditions such as heat and moisture, and also stressed the importance of competition for resources as a factor in determining plant distributions. His work on these abiotic and biotic limiting factors led to his recognition of distinct floral geographic regions. His ideas on competition also led him to develop the concept of "nature's war," which Charles Darwin would later use in his principle of natural selection.

Figure 2.4: Alexander von Humboldt, the "father of phytogeography" (Wikipedia 'Alexander von Humboldt;' Attribution: [http://www.avh.de/en/stiftung/namenspatron/portrait.htm)](http://www.avh.de/en/stiftung/namenspatron/portrait.htm)

2.5 HOW OLD IS THE EARTH?

As the 18th century came to a close, biogeographical knowledge was accelerating, but was still primarily descriptive in nature. The "how and why" explanations for the patterns found by these early naturalists were still elusive. One major impediment to progress was a lack of understanding and acceptance of the ancient age of the Earth. At this time, it was still commonly thought by most people, including many naturalists, that the Earth was only a few thousand years old, based on biblical interpretations. But by the late 18th and early 19th centuries, some geologists were challenging this view.

Charles Lyell (1797–1875), the "father of geology," was the most prominent of these (Fig. 2.5). Lyell was a proponent of "uniformitarianism," a view which, among other things, asserted that the Earth's geological features are the result of gradual processes such as erosion and uplift that take place very slowly and over very long periods of time. Furthermore, these processes and rates were the same in the past as in the present. This was in contrast to proponents of "catastrophism," who believed that geological features are primarily the result of short-lived but violent events that were more common and intense in the past. Uniformitarianism led Lyell to the inevitable conclusion that the Earth is much older than a few thousand years; incredibly long periods of time were required to produce the present day geological features of the Earth. Lyell was convinced that the Earth was several hundred million years old; we now know even that was a vast underestimate of the Earth's age. Many of the patterns observed in the biological world were incongruous with the young-Earth view. Acceptance by the scientific community of the ancient age of the Earth paved the way for new and exciting ideas in biogeography.

Figure 2.5: Charles Lyell, the "father of geology"
(Wikipedia 'Charles Lyell'; Attribution: 1840 painting by Alexander Craig)

2.6 DARWIN, WALLACE, AND EVOLUTION

Sir Isaac Newton once said “if I have seen further than others, it is by standing upon the shoulders of giants.” **Charles Darwin** (1809–1882) would likewise stand on the shoulders of the scientific giants mentioned in the preceding paragraphs. As a young man in his 20s, Darwin (Fig. 2.6) would embark on a voyage of discovery that would revolutionize our view of life. This voyage began in 1831, when Darwin was invited to serve as naturalist and a companion to Captain Robert FitzRoy on board the HMS *Beagle*. This five-year voyage circumnavigated the Earth, sailing from England across the Atlantic, along the coast of South America and returning via Australia and South Africa (Fig. 2.7). During this voyage, Darwin collected many rocks, fossils, plants, and animals, particularly in South America and the Galápagos Islands. Preceding the voyage, Darwin firmly believed in the literal truth of the Bible and its account of creation, and fully expected to find this truth reflected in the natural world – that the same or similar species would be found in geographically separate locations that had similar environments, as Linnaeus had predicted.

Figure 2.6: Charles Darwin, whose voyage aboard the HMS *Beagle* would lead him to the theory of evolution by natural selection (Wikipedia ‘Charles Darwin;’ Attribution: Late 1830s portrait by George Richmond, from *Origins*, Richard Leakey and Roger Lewin)

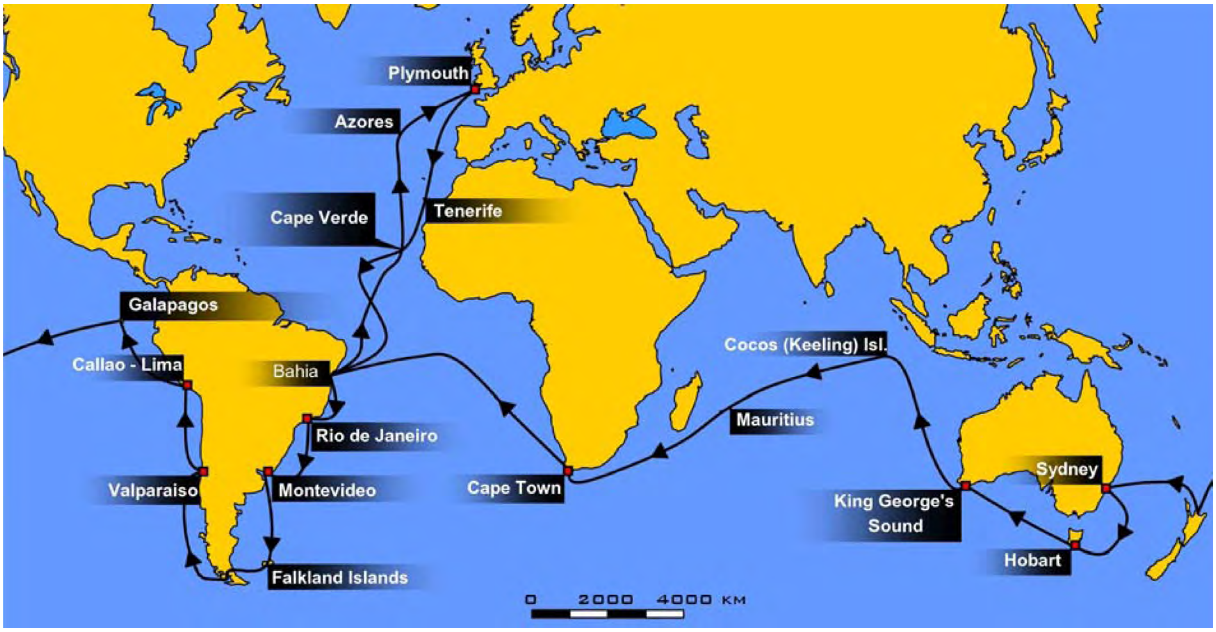


Figure 2.7: Charles Darwin's voyage on the HMS *Beagle* (Wikipedia 'Second voyage of HMS *Beagle*;' Attribution: Webmaster at the German language Wikipedia)

However, Darwin consistently found the opposite – similar species tended to occur in close geographic proximity, regardless of differences in environment. The bird life of the Galápagos Islands serves as an example. On the islands, Darwin collected birds that he thought represented a variety of groups such as blackbirds, wrens, grosbeaks, and finches. He preserved these birds and, upon returning to England, gave them to the famous ornithologist John Gould for identification. Darwin was surprised to learn that these birds represented several species of an odd group of ground finches found nowhere else on Earth, but which were closely related to finches found on the South American continent. Darwin's logical conclusion was that an ancestral South American species had colonized the Galápagos, and then over time radiated and adapted to the various available ecological niches on the islands. This adaptive radiation was particularly evident in the sizes and shapes of the finches' beaks, reflecting adaptation to various food sources.

Fig. 2.8 illustrates this in four of the species. The large ground finch (#1 in the figure), with its massive beak, specializes in cracking and eating large, tough seeds it finds on the ground. The medium ground finch (#2 in the figure), with a smaller but still stout beak, also eats seeds, but a greater variety, and its smaller beak gives it greater flexibility to supplement this diet with a variety of other foods such as leaves, buds, and insects. The small tree finch (#3 in the figure) has a beak that is smaller still and slightly curved, well adapted for grasping its primary food, insects, off of the surfaces of leaves and branches, and also to bite through small stems to get to the insects inside. The green warbler finch (#4 in the figure) uses its thin, pointed beak to probe in plant litter, mosses, etc. for insects and spiders.

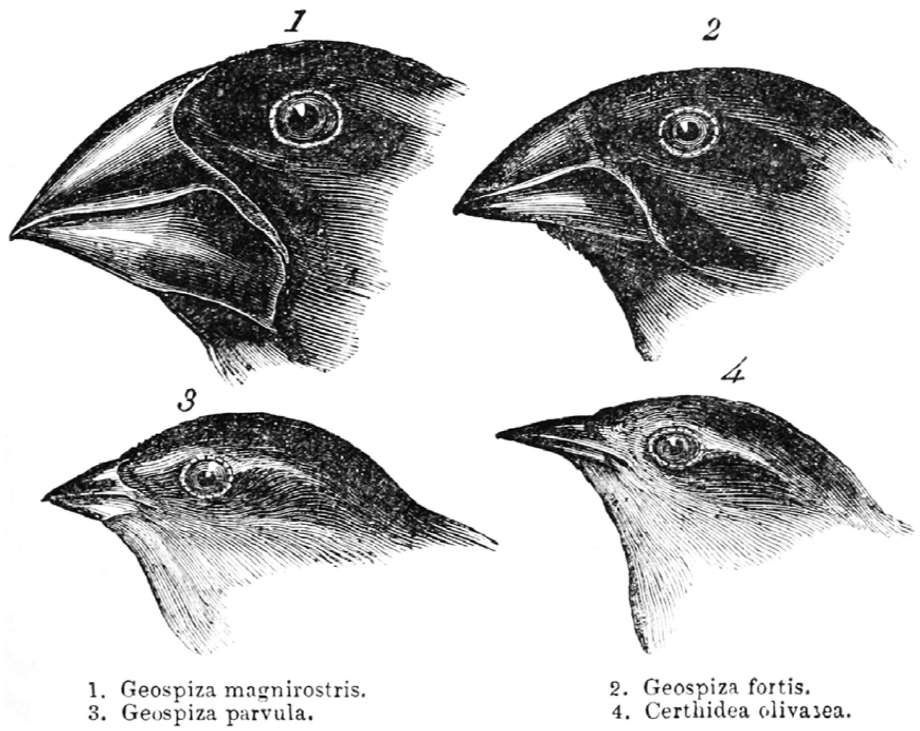
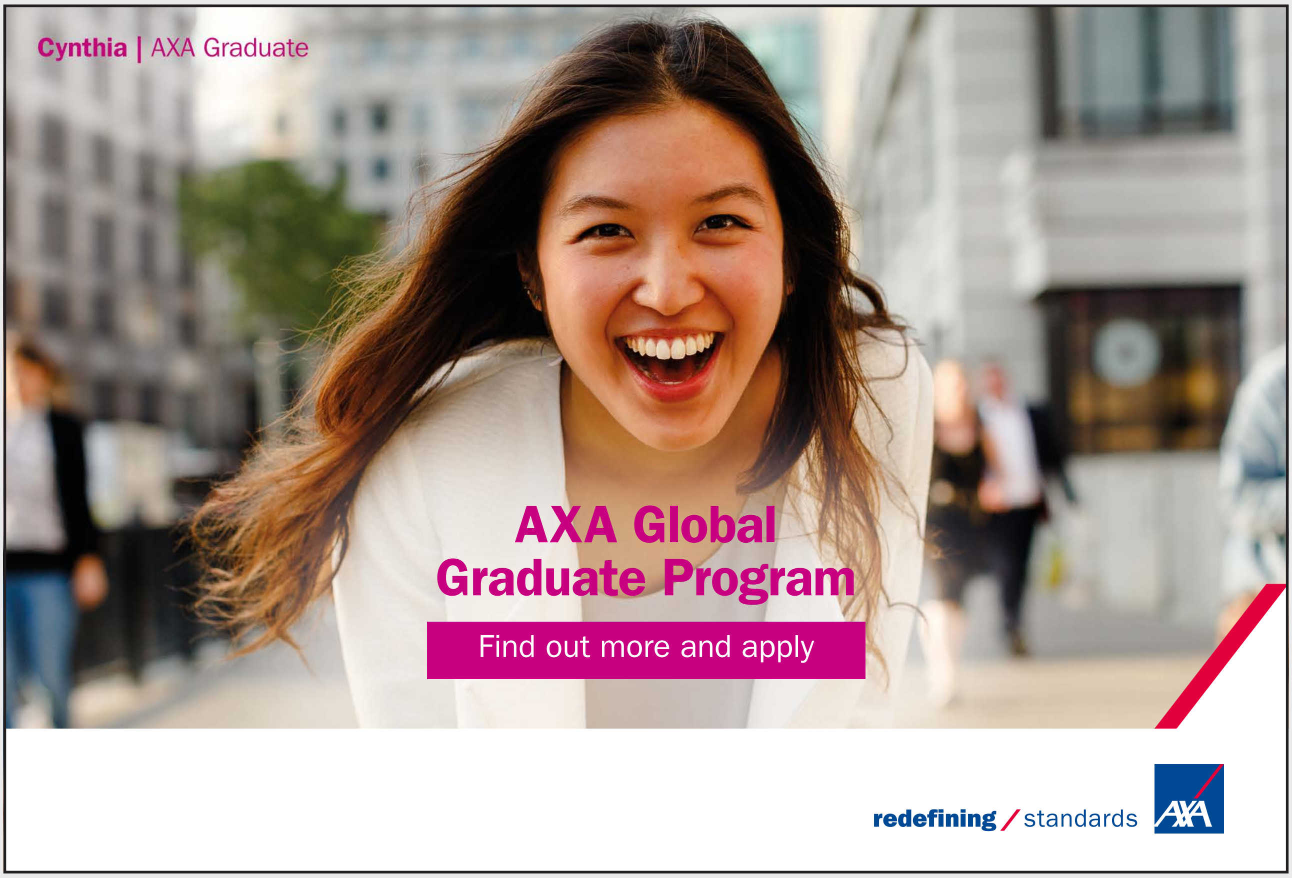


Figure 2.8: Four species of Darwin's finches (Wikipedia 'Darwin's finches;' Attribution: *Journal of Researches into the Natural History and Geology of the countries visited during the voyage of H.M.S. Beagle round the world,* http://biodiversitylibrary.org/page/2010582)



Although Darwin considered the fossil record too incomplete to provide a very detailed record of evolution, he did point out that fossils in more recent geological strata were more similar to living organisms than were fossils in deeper strata. He also noted that fossil mammals in a particular area are more closely related to living mammals of that area than to fossils from the same stratum in different geographical regions, again suggesting that living species were descended from extinct species that had existed in the same location.

By the time Darwin returned to England in 1836, he was becoming convinced that species evolve from pre-existing ones. However, he still did not know of a mechanism by which this could occur. He read Thomas Malthus' *An Essay on the Principle of Population*, in which Malthus pointed out that unchecked population growth would inevitably outstrip the food supply. Darwin connected Malthus' work with Augustin de Candolle's earlier ideas on "nature's wars," the struggle for existence among organisms. Darwin thus recognized the following facts:

- Individuals in a population vary
- Much of this variation is inherited
- In any population, a large proportion of offspring die before reaching reproductive age

From these facts, Darwin concluded that, since organisms vary in their biological traits, some of these traits must be advantageous and therefore give those individuals that possess them an "edge" in survival and reproduction. These individuals would on average produce more offspring, and their advantageous traits would increase in the population. The concept is straightforward, but the implications profound; indeed, the theory of evolution by natural selection is one of the most important scientific advances in history, and is the unifying theory of biology. Philosopher of science Daniel Dennett, in his book *Darwin's Dangerous Idea*, stated that "If I were to give an award for the best single idea anyone ever had, I'd give it to Darwin, ahead of Newton and Einstein and everyone else. In a single stroke, the idea of evolution by natural selection unifies the realm of life, meaning, and purpose with the realm of space and time, cause and effect, mechanism and physical law." While an award for "best idea ever" is certainly open for debate, there can be no doubt that the theory of evolution by natural selection ranks with the most brilliant and revolutionary ideas in history.

It was over two decades after Darwin returned to England before he published the first edition of his famous book, *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*, in 1859. Reasons for this delay may have included illness and uncertainty over the reception it might receive, but Darwin was also busy with family life as well as other professional projects and obligations. But this delay in publication of his theory almost caused Darwin to be "scooped." Another accomplished naturalist, **Alfred Russel Wallace** (1823–1913) combined his observations in South America and the Malay Archipelago with Malthus' ideas on population growth to formulate the theory of evolution by natural selection. In his autobiography, Wallace (Fig. 2.9) relates how he thought of Malthus and natural selection while bedridden with fever in the East Indies.

Wallace and Darwin corresponded with each other, and each influenced the thinking of the other. During these correspondences, Wallace sent Darwin an essay outlining his ideas, which Darwin immediately recognized as very similar to his own. The details of what happened next are sketchy. Darwin passed the manuscript along to his friend Charles Lyell, but there is disagreement among scholars about whether he did this immediately, or held Wallace's manuscript for weeks. It is difficult to know what was going through Darwin's mind. If Wallace's manuscript were published, it would take precedence; Darwin's originality and life's work would be trumped. Through the intervention of Charles Lyell and Joseph Hooker, it was arranged for Wallace's essay to be read along with some of Darwin's writings at the 1858 Linnaean Society of London meeting, thus assuring joint credit for the theory. Wallace may forever be known as the answer to a favorite biology trivia question, "who was the other guy?" But there is no need to feel sorry for Alfred Russel Wallace, for he would become known to history as a preeminent scientist and naturalist in his own right. Wallace would publish twenty books and 500+ scientific articles, and would develop biogeographical concepts and principles that are still important today. His contributions to the field of biogeography are so important that many consider him to be the "father of biogeography."

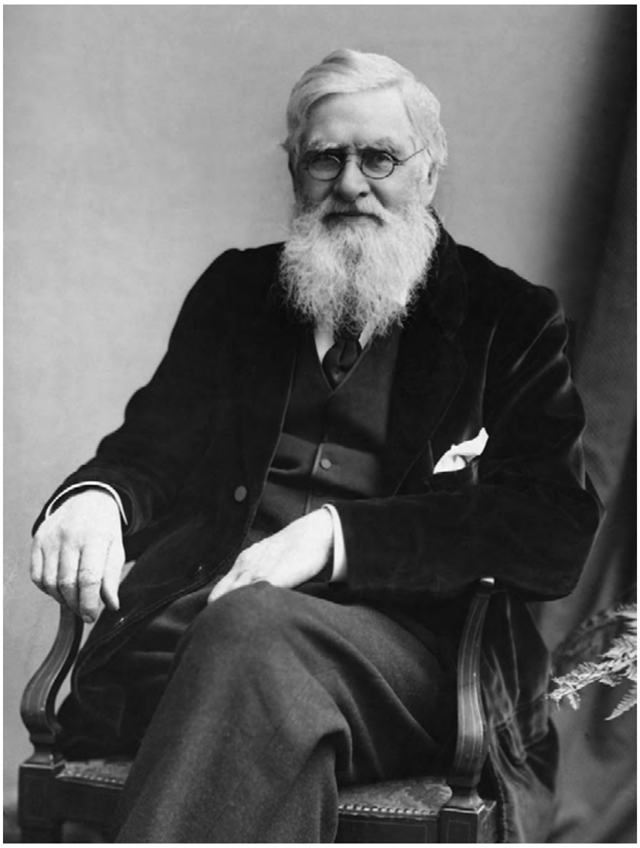


Figure 2.9: Alfred Russel Wallace, who many consider the "father of biogeography;" he independently conceived the theory of evolution by natural selection (Wikipedia 'Alfred Russel Wallace;' Attribution: London Stereoscopic & Photographic Company, in Borderland Magazine, April 1896)

2.7 EXPLAINING DISJUNCTIONS

By the late 1800s, scientists such as Lyell, Darwin, Wallace, and others had provided convincing evidence that the Earth was ancient and that species change over time, thus overcoming two worldviews that were limiting the progress of the science of biogeography. But perplexing questions remained. In particular, certain unusual distributions, known as "disjunct" distributions, presented a problem. A **disjunct** distribution is a distributional pattern in which the range of a taxonomic group is discontinuous, with wide geographical separations. How did such distributions occur? This was difficult to explain. Some biogeographers, such as Darwin, invoked dispersal as the major mechanism by which disjunctions occurred. While the dispersal abilities of many taxonomic groups are impressive, this seemed insufficient as an explanation for distributions such as that of the fossil plant genus *Glossopteris* (Fig. 2.10), a Permian seed fern which is widespread in South America, Africa, Madagascar, India, Antarctica and Australia. These plants were woody, seed-bearing shrubs or trees, some of which reached 30 m in height. Barriers to dispersal from continent to continent seem unsurmountable. The seeds of this plant are too large to have been dispersed by wind, and unlikely to have floated across the ocean.

Figure 2.10: Fossils of *Glossopteris*, a Permian seed fern with a disjunct southern hemisphere distribution (Wikipedia '*Glossopteris*;' Attribution: Daderot)

Charles Lyell and others suggested that such distributions were the result of ancient land bridges which had connected the continents but had since submerged. In particular, the British botanist **Joseph Hooker** (1817–1911) studied the distributions of Southern Hemisphere flora extensively, but couldn't accept dispersal as an explanation for the disjunct distributions he observed. As was the case with other scientists of the day, Hooker believed that the positions of the continents were fixed, and concluded that ancient land bridges were the most logical explanation. But Darwin and the dispersalists found these post-hoc explanations, with little or no supporting evidence, unconvincing.

Such distributions would elude explanation until the early 1900s, when arguments for the possibility of continental movement, led by the German geophysicist and meteorologist **Alfred Wegener** (1880–1930), gained momentum. Wegener's theory of continental drift was first published in 1912 and revised periodically until his death in 1930 on a research expedition in Greenland. Wegener (Fig. 2.11) provided compelling biological and geological evidence for continental movement, but despite the strength of his arguments and the weaknesses of the opposition's, his theory was not generally accepted until over 30 years after his death. Acceptance of Wegener's theory was hampered by lack of a known mechanism by which the continents could move, but also by the close-mindedness and lack of imagination of entrenched "establishment" scientists. The fact that Wegener was not a geologist but an "outsider" (atmospheric scientist) did not help matters in the latter respect. It wasn't until the 1960s, over 30 years after his death, that irrefutable geological evidence made denial of Wegener's theory (now known as the theory of plate tectonics) untenable for even the most diehard opponents. Acceptance of the dynamic nature of the Earth's landmasses would clarify the enigmatic distributions of *Glossopteris* and other taxa with southern hemisphere or "gondwana" distributions (Fig. 2.12).

Figure 2.11: German geophysicist and meteorologist Alfred Wegener, who is best known for his theory of continental drift (Wikipedia 'Alfred Wegener;' Attribution: Loewe, Fritz; Georgi, Johannes; Sorge, Ernst; Wegener, Alfred Lothar)

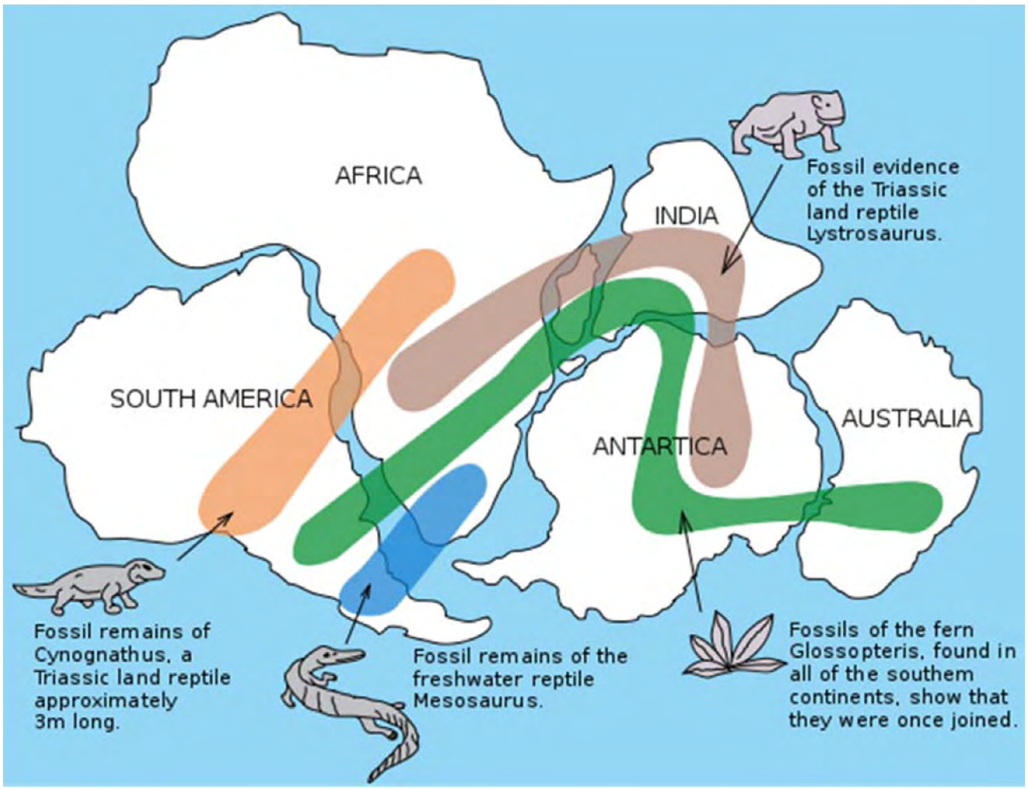


Figure 2.12: Gondwana distributions of several taxa on continents that are now widely separated, suggesting they were once connected (Wikipedia 'Alfred Wegener;' Attribution: United States Geological Survey)

2.8 LATE 20TH CENTURY PROGRESS

The last half-century has witnessed increased importance of biogeography as a major field of interdisciplinary research. The 1966 publication of *Phylogenetic Systematics* by German entomologist **Willi Hennig** (1913–1976) brought to the forefront the cladistics approach to biogeographical classification. In cladistics, evolutionary relationships of taxa are uncovered based on shared unique characteristics present in the most recent common ancestor but not in earlier ancestors. This approach would prove to be an important bridge between evolutionary biology and biogeography. Likewise, the application of molecular genetics approaches has made it possible to investigate evolutionary and biogeographical patterns in the relatively recent past. Phylogeography, an approach developed by **John Avise** (1948–), focuses on geographically structured genetic patterns among populations within a species, and has many applications in conservation biology, public health, and even the study of language origins.

Another major development in the last half of the 20th century was the maturation of the science of ecology and its integration with biogeography. Important work in ecological biogeography in the 1960s and 70s focused on the biotic and abiotic factors that influence the distribution of biological diversity. Important research in ecological biogeography also included seminal studies in the area of island biogeography by two of the most influential biologists of the 20th century, the late **Robert MacArthur** (1930–1972) and **Edward O. Wilson** (1929–).

Marine biogeography might be thought of as the "final frontier" in the field of biogeography. In general, we know much less about the organisms that inhabit the oceans than we do about terrestrial organisms. This is understandable because it is much more difficult to observe and sample marine organisms, particularly those that are great distances from land, or at great depths. As a consequence, knowledge of marine biogeography has grown much more slowly and recently than knowledge of terrestrial biogeography. But the pace of growth of our knowledge of marine distributions is increasing, thanks to a great extent to increased abilities to explore the deeper regions of the ocean as well as satellite technology that has revealed patterns in the distributions of oceanic planktonic life.

The history of the growth of biogeography reflects the integrative and multidisciplinary nature of the field. From basic early descriptions of animal and plant distributions the science has developed explanatory power that can help address some of today's most pressing environmental problems. In the rest of this book we will review in more detail the principles of biogeography and their applications to today's challenges.

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3 MAPS, RANGES, AND GEOLOGICAL CHANGES

Your goals for this chapter are to learn about:

- The three basic categories of map projections
- The usefulness and limitations of geographic range maps
- Evidence for the theory of plate tectonics
- Pangea, Laurasia, and Gondwana
- Climatic effects of plate tectonics

3.1 INTRODUCTION

The science of biogeography focuses on the distribution of biodiversity across the globe. But before we can intelligently address the distribution of biodiversity, there are two fundamental questions we must address that relate to this focus: 1) how do we represent the surface of the earth on a two-dimensional surface so that we can adequately communicate information about these distributions, and 2) how and why does the surface of the earth (and therefore, our representations of it) change over time. These two questions will be the subject of this chapter.

3.2 MAP PROJECTIONS

All of us use maps in a variety of ways – to get from one place to another without getting lost, to estimate the distance between two points, to find the location of an unfamiliar place where an important social or political event is taking place, and, in the case of biogeographers, to study the distribution of biodiversity. But have you ever wondered how maps are made, or thought about exactly what information is being conveyed by a map? A **map** can be defined as a two-dimensional representation of the Earth. But, as most of us are now aware, the Earth is not flat. So how can we represent the surface of a roughly spherical object on a flat surface? A map projection is the "flattening" of a curved surface into a plane.

As the famed German mathematician Carl Gauss (1777–1855) proved, a curved surface cannot be represented on a plane without distortion. The type of distortion varies with the type of map projection. There are many varieties of map projections, but most fall into three broad categories: cylindrical, conic, and azimuthal. There is no single, objectively "best" map projection; the usefulness of any given type of projection depends on the use for which it is intended.

A **cylindrical projection** of the earth can be imagined as a projection of the earth onto a cylindrical sheet of paper, with the cylinder tangentially touching the earth at, for example, the equator. A well-known cylindrical projection is the standard Mercator projection (Fig. 3.1). In this projection, objects such as landmasses are distorted as one moves from the equator toward the poles. For instance, Greenland appears much larger than Australia in Fig. 3.1. However, comparing the true area of the two landmasses, we see that in reality Australia is over 3.5 times as large as Greenland (Fig. 3.2). Fig. 3.3 shows Tissot's indicatrix, which indicates the distortion at various points for, in this case, the standard Mercator projection. On a spherical globe, the dots would all be equal sizes.

Figure 3.1: Mercator projection of the world between 82°S and 82°N (Wikipedia 'Mercator projection;' Attribution: Daniel R. Strebe, August 15, 2011)

Figure 3.2: Comparison of actual land areas of Australia and Greenland (Wikipedia 'Mercator projection;' Attribution: Benjamin Hell (User: Siebengang))

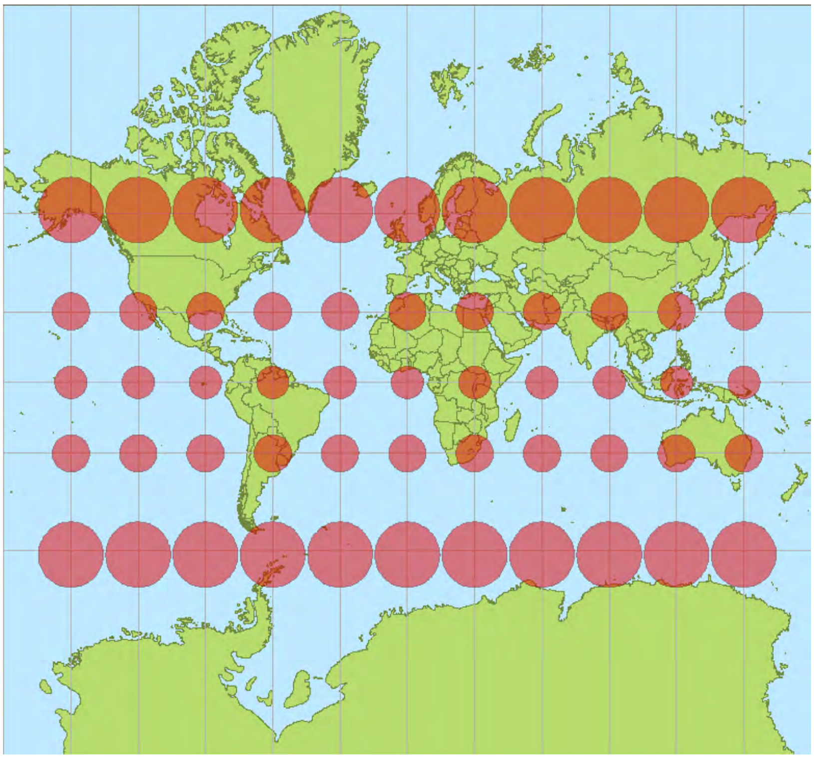

Figure 3.3: Tissot's Indicatrices on the Mercator projection; on a spherical globe, the dots would all be equal sizes (Wikipedia 'Mercator projection;' Attribution: Stefan Kühn)

In **conic projections**, we can visualize a conical sheet of paper intersecting the earth at two standard parallels, resulting in little distortion between the parallels, but increasing distortion with distance away from the parallels. For instance, in an Albers conic projection using standard parallels of 20°N and 50°N, North America is depicted with little distortion, but southern hemisphere landmasses are increasingly distorted, particularly in an east-west direction (Fig. 3.4). **Azimuthal projections**, which can be visualized as a flat sheet of paper contacting the globe at a central point, provide an accurate depiction of regions near the central point and distances/directions from the central point, but elsewhere shapes and sizes become distorted (Fig. 3.5).

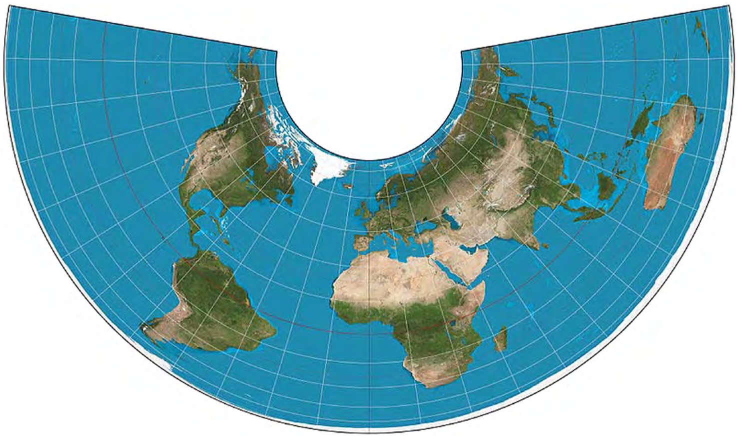

Figure 3.4: Albers projection of the world with standard parallels 20°N and 50°N (Wikipedia 'Albers projection;' Attribution: Daniel R. Strebe, August 15, 2011)

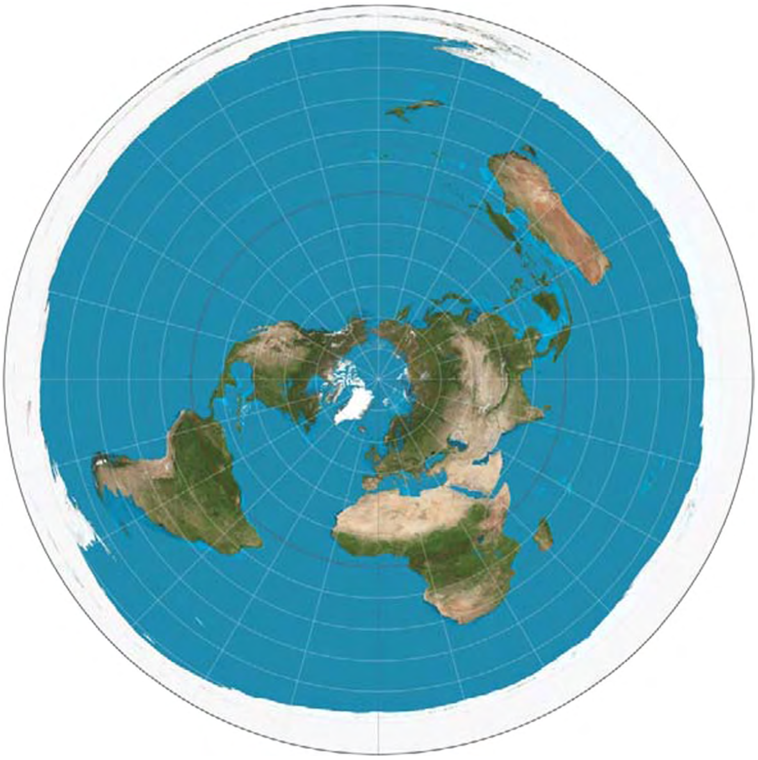

Figure 3.5: Polar azimuthal equidistant projection (Wikipedia 'Azimuthal equidistant projection;' Attribution: Daniel R. Strebe, August 15, 2011)

For large-scale maps, the transverse Mercator projection, a variant of the standard Mercator projection, is probably the most commonly used. For the transverse Mercator projection, the axis of the cylinder lies along the equatorial plane, and the line of tangency is any chosen meridian, which is designated as the central meridian. This projection allows construction of highly accurate large-scale maps anywhere on Earth. For smaller-scale maps that include whole continents or even the entire world, a variety of projections are used, depending on the purpose of the map.

3.3 GEOGRAPHIC RANGES AND RANGE MAPS

Once the type of map for a given purpose and geographic location has been chosen, a range map, which represents the geographic distribution of a taxonomic group, can be constructed. There is a variety of factors, at ecological as well as evolutionary time scales, that determine the geographic range of an organism. These include such abiotic factors as temperature, humidity, soil moisture and pH, and nutrient availability, as well as biotic interactions such as competition, predation, parasitism, and mutualistic associations. Human activities and anthropogenic climate change have the potential to affect geographic ranges on a global scale.

Knowing the distributions of organisms is important for a variety of reasons. As we saw in the last chapter, knowledge of geographic ranges provides insight into the evolutionary history and evolutionary relationships of organisms. Such knowledge is also critical in conservation efforts. In particular, as human activities continue to affect the abundance and distributions of other organisms, documentation of geographic ranges allows us to assess and possibly mitigate these effects. Information on geographic ranges, such as that found in popular field guides, also helps promote interest in conservation among the general citizenry by helping them to become familiar with the biodiversity in their geographic region.

There are different approaches to mapping geographic ranges of organisms, and these approaches can differ considerably in their degree of detail. It is important to recognize the limitations and usefulness of these different types of range maps. For instance, a map providing only an outline of the geographic range of the Eurasian lynx, *Lynx lynx* (Fig. 3.6), gives one a general idea of where the species is found over a large geographic area. But of course these cats are not uniformly distributed throughout their range, and the map provides no information regarding the relative abundance of the species in different locations within its range, which varies from relatively abundant in Siberia to very low in parts of Europe. Some range maps provide more detail by using such approaches as dots or contour lines/colors to depict the relative abundances of organisms within the geographic range. But such information must be available before it can be incorporated into a range map, and for the vast majority of species, particularly small-bodied, hyper-diverse groups such as many invertebrate taxa, such detailed information is lacking.

Figure 3.6: Eurasian lynx and its geographic range (Wikipedia 'Eurasian lynx;' Attribution: mpiet (http://www.mindbox.at/gallery/))

Using range maps, there are several terms that biogeographers commonly use to describe the occurrence of a taxon in space and time. An **extinct** taxon is one that no longer has living members, whereas an **extant** taxon contains living members. An **endemic** taxon is one that is only found in one location or geographic area. For instance, emus are endemic to Australia. A taxon that is found in geographic areas that are separated from each other (i.e., has a discontinuous range) is said to have a **disjunct** distribution. The extinct *Glossopteris*, discussed in chapter 2, exhibits a disjunct gondwana distribution. The extant Kerry slug, *Geomalacus maculosus*, is widespread in Spain and Portugal, but also has disjunct populations in County Kerry, southwestern Ireland. A **relict** taxon is one that "has seen better days" and was once more geographically widespread or taxonomically diverse. The thylacine, or Tasmanian tiger, survived as a relict population on the island of Tasmania until the 1930s, even though it had disappeared from mainland Australia centuries earlier.

3.4 THE DYNAMIC EARTH

As noted in Chapter 2, the belief in a static Earth was a major impediment to progress in the science of biogeography. But in the early 1900s, Alfred Wegener (Fig. 2.11) drew upon evidence such as the "gondwanan distributions" of certain fossils (Fig. 2.12), patterns of coal deposits, and stratigraphy (layering) of rocks along coastlines to propose the theory of continental drift. However, for reasons outlined in Chapter 2, it was decades before Wegener's theory was accepted by the scientific community. The famous broadcaster and naturalist Sir David Attenborough relates an experience that he had at his university in the 1940s. When he asked one of his lecturers about Wegener's theory, the lecturer replied that "the idea was moonshine." (McKie, Robin; 28 October 2012; "David Attenborough: Force of Nature;" *The Observer* (London)). It wasn't until the 1960s that Wegener's ideas were widely accepted. Two lines of evidence supported Wegener's theory: 1) paleomagnetism, and 2) seafloor spreading. Paleomagnetism refers to the existence of magnetized particles in rocks. These magnetized particles align themselves with the Earth's magnetic field, and the orientation of the particles is locked in when the rocks harden. Thus, the position of the rock relative to the magnetic field at the time of solidification is preserved. If the Earth's landmasses have not moved relative to each other, then all the magnetic particles should be oriented in the same direction. Instead, these particles vary in their orientation based on the ages of the rocks, and provide a record of the pathways of movement of the continents over time.

The second, and even more compelling source of evidence, was the discovery of the existence of spreading ridges, where new seafloor is formed, and trenches, where the old seafloor disappears into the Earth. Thus, the Earth's surface is composed of a number of tectonic plates (Fig. 3.7). The spreading ridges and trenches produce something of a "conveyor belt effect," moving the plates that contain ocean floor and continents relative to each other or, where a ridge exists under a continent, splitting the continent. The rate of movement varies among the different tectonic plates, but is said to average about 2.5 cm per year, or about the same rate that your fingernails grow. However, over the course of hundreds of millions of years, this slow rate of movement produces dramatic changes in the positions of the continents. Because the age of the seafloor varies depending on time of formation, positions of the continents at a given time in geological history can be estimated by removal from the map of any seafloor produced since that time. Because seafloor older than about 180 million years has disappeared into the trenches, paleomagnetism must be used to estimate continental positions before that time.

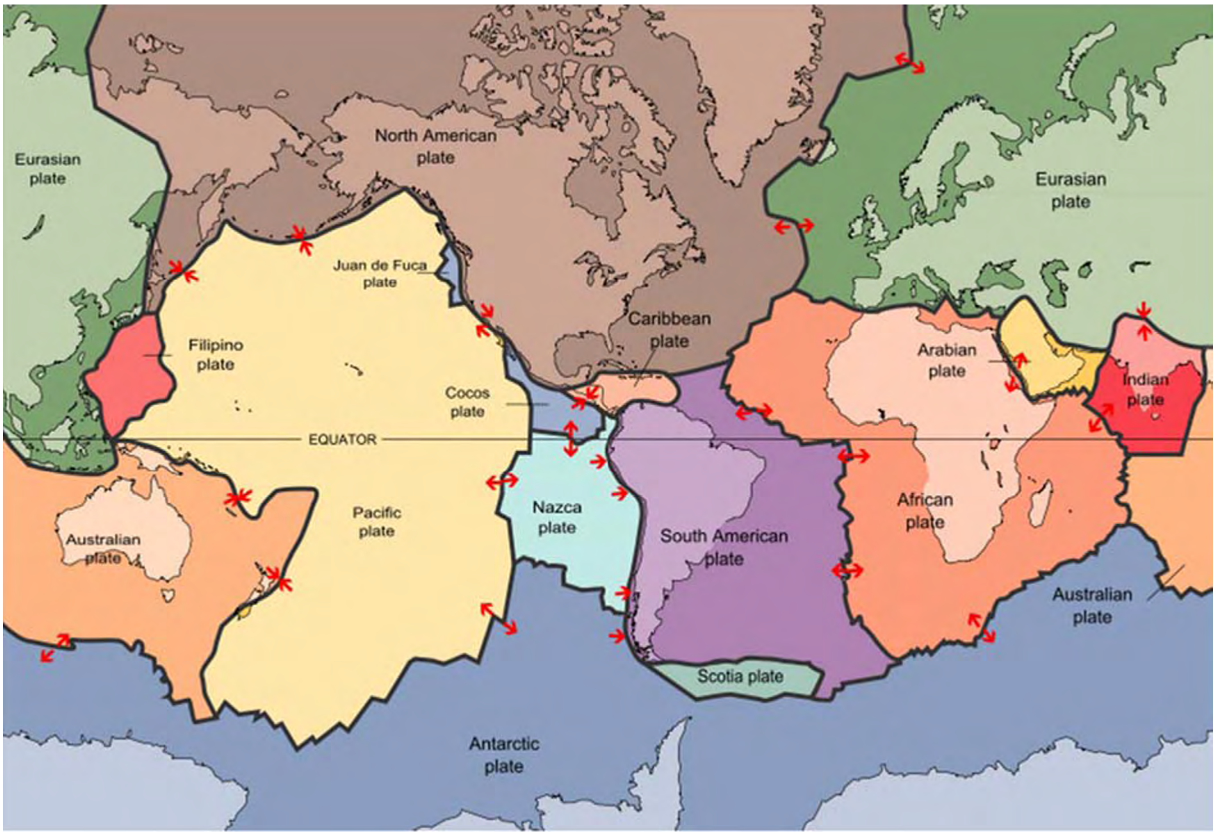

Figure 3.7: The tectonic plates of the world (Wikipedia 'Plate tectonics;' Attribution: United States Geological Survey)

The dramatic changes that have taken place with regard to the positions of the continents are illustrated by their positions at various time points during relatively "recent" geological history. If we look at the Earth about 300 million years ago, in the late Carboniferous, the Earth's landmasses formed a large supercontinent, Pangea (Fig. 3.8), surrounded by a "super ocean," Panthalassa. By about 200 million years ago, at the Triassic/Jurassic boundary, the landmasses were separating into two supercontinents (Fig. 3.9). The northernmost one, Laurasia, would drift northward after the split. It contained most of the landmasses that presently occupy the northern hemisphere. The southernmost supercontinent, Gondwana, included most of today's southern hemisphere landmasses, and after its separation from Laurasia would drift further south.

Figure 3.8: Map of Pangaea with modern continental outlines (Wikipedia 'Pangaea;' Attribution: en:User:Kieff)

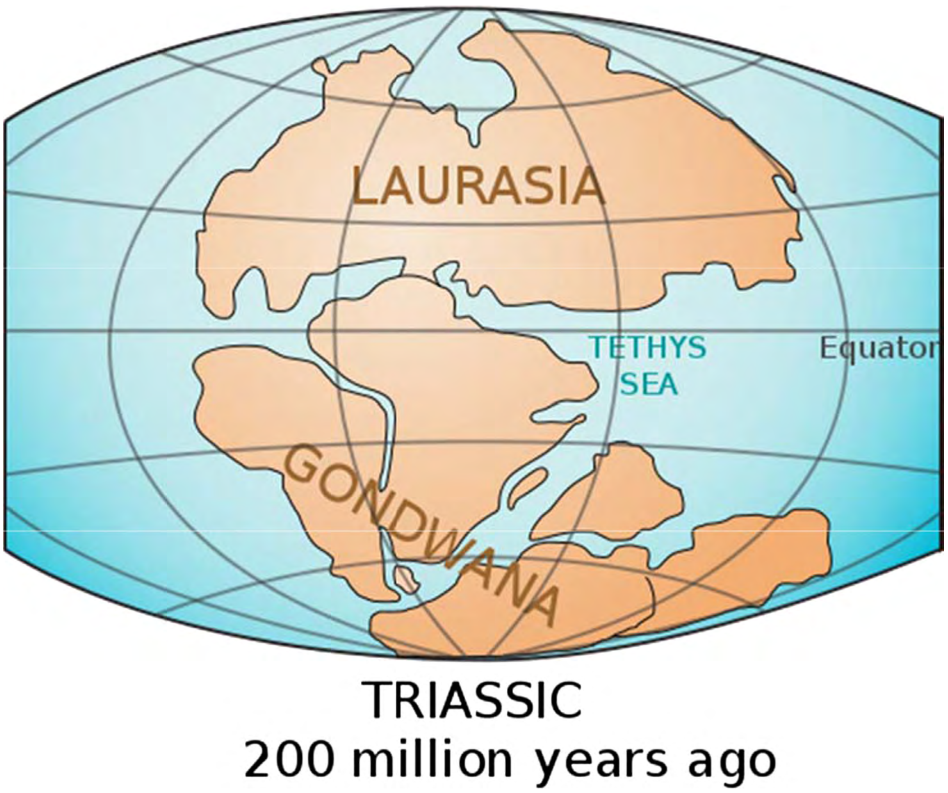

Figure 3.9: Map of Laurasia and Gondwana in the late Triassic/early Jurassic (Wikipedia 'Laurasia;' Attribution: User:LennyWikidata)

Plate tectonics and the movements of the continents affect the Earth's dynamics in many different ways, particularly climatically. As the landmasses change latitudinal positions, their climate changes as a result of increased or decreased direct solar radiation. During periods when landmasses are located at the poles, the formation of ice sheets increases the Earth's **albedo**, or reflectivity. A higher albedo means reduced absorption of solar radiation, resulting in cooling of the Earth and potential increased glaciation. Joining and separation of landmasses also affects the influence of oceans on climate; large contiguous landmasses tend to have more continental climatic conditions in the interior regions that are far away from coastlines, whereas the climates of smaller landmasses are more subject to the ocean's influence. Continental movements also affect patterns of ocean currents, and tectonic formation of mountain ranges affects climate through the formation of rain shadows and other effects.

As mentioned in Chapter 1, the discipline of biogeography pulls together two of the most important theories in science: the theory of plate tectonics, and the theory of evolution by natural selection. An understanding of the interplay between these two forces is essential to an understanding of the past and present distributions of biological diversity. In the next chapter, we will examine the theory of evolution by natural selection.

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4 EVOLUTION – DESCENT WITH MODIFICATION

Your goals for this chapter are to learn about:

- Early evolutionary ideas and thinkers
- The hypothesis of inheritance of acquired characteristics and its rejection
- Mechanisms of evolution
- The theory of evolution by natural selection
- Types of natural selection
- Types of speciation
- Reproductive isolating mechanisms

4.1 INTRODUCTION

The theory of evolution by natural selection is the bedrock theory of biology, and is fundamental to an understanding of the geographic distribution of biological diversity. As the renowned evolutionary biologist Theodosius Dobzhansky famously stated, “nothing in biology makes sense except in the light of evolution.” This statement is equally true for biogeography as well. In this chapter, we will briefly review some of the earliest pre-Darwinian ideas regarding biological evolution before moving to a discussion of modern evolutionary theory and its implications.

4.2 EARLY EVOLUTIONARY THOUGHT

At the most basic level, “evolution” simply means a pattern of change over time. The concept of biological evolution is forever linked to Charles Darwin and Alfred Russel Wallace, but the idea that populations and species change over time actually predates these two biologists. Pre-Socratic philosophers such as **Anaximander** (610–546 BC) and **Empedocles** (490–430 BC) viewed animals and plants as products of change or recombination over time. Empedocles specifically introduced the idea of chance into the equation. These views contrasted to those of later philosophers such as **Plato** (ca. 428–348 BC), **Aristotle** (384–322 BC) and **Zeno** (334–262 BC), who proposed that species did not change because they were perfectly designed. These **teleological** explanations of design with purpose would become influential in Christian philosophy over a century later. In contrast to Christianity, adherents of eastern philosophies and religions have had an easier time accepting the concept of biological evolution, and incorporating it into their belief systems. Taoism, for example, rejects the concept of biological immutability, and Taoist philosophers such as **Zhuang Zhou** (c. 369–286 BC) believed that species developed varying characteristics as a result of living in different environments. Later, the Islamic world would also produce forward-thinking individuals who anticipated evolutionary thought. Probably the most advanced of these was the Persian scientist and philosopher **Nasir al-Din al-Tusi** (1201–1274; Fig. 4.1), who even recognized the unity that humans share with the rest of the biological world.

Figure 4.1: Early Persian scientist and philosopher Nasir al-Din al-Tusi (Wikipedia 'Nasir al-Din al-Tusi;' source unknown)

Other scientists noted patterns in the variation among species and attempted to provide explanations for these patterns. One such notable explanation involved "inheritance of acquired characteristics," an idea generally associated with the French naturalist **Jean-Baptiste Lamarck** (1744–1829; Fig. 4.2). In this view, physical changes acquired by an organism over the course of its lifetime can be passed on to its offspring. A classic example is that of giraffe evolution; according to the concept of inheritance of acquired characteristics, early giraffes continually stretched their necks to reach higher and higher tree branches. This made their necks longer and stronger, and these characteristics were then passed on to their offspring. Inheritance of acquired characteristics was a widely accepted idea for decades, but greater understanding of the mechanisms of inheritance led to rejection of this idea by the early 1900s. Even so, Lamarck's efforts in providing a theoretical framework for biological evolution paved the way for further advances in the field.

Figure 4.2: French naturalist Jean-Baptiste Lamarck (Wikipedia 'Jean-Baptiste Lamarck;' Attribution: 1802–03 painting by Charles Thévenin)

4.3 MECHANISMS OF EVOLUTION

As the title of this chapter suggests, a good working definition of biological evolution is "descent with modification." Knowledge of genetics as the basis of inheritance was not widely known in Darwin's time, but now we have a more specific definition of evolution: change in allele frequencies in a population. There are several mechanisms by which this occurs:

- Mutation – a change in the sequence of bases in an organism's DNA. A mutation is important in evolution only if it is passed to future generations, thus providing increased genetic diversity and the raw material on which natural selection can act.

- Genetic drift – change in allele frequencies within a population as a result of chance. Genetic drift is particularly important in small populations, in which random genetic events have disproportionately large effects. For example, if a particular allele is rare in a small population, and none of the few individuals who have this allele reproduce, then that allele completely disappears from the population, and genetic variation is reduced. Two special cases in which genetic drift is important are 1) the founder effect, and 2) genetic bottlenecks. In the founder effect, a small number of individuals disperse from their original population and found a new, isolated population. This new population may have allele frequencies that are not representative of the original population; certain traits may be more or less frequent in the new population. One well known example of this is the frequency of the recessive allele for Ellis-van Crevald syndrome among Pennsylvania Amish, which is much higher than that of the larger parent population in Switzerland. Genetic bottlenecks occur when a population undergoes a dramatic decline, resulting in the random elimination of many alleles from the population. This results in long-term loss of genetic diversity, even if the population recovers. Cheetahs provide a classic example. In the last 10,000 years, habitat change due to climate and human persecution in the 1800s have driven cheetah numbers down to a few thousand individuals, resulting in highly inbred, low diversity populations.

- Migration – when individuals enter (immigrate) or leave (emigrate) a population, they bring or take their alleles with them. If their allele frequencies are not representative of the population as a whole, this results in change in allele frequencies in the population.
- Natural selection – individuals with certain alleles have more offspring. This changes the allele frequencies in a population by favoring those that contribute to survival and reproduction and selecting against those that do not. This mechanism of evolution is the most important in shaping the adaptations of populations to their environments and has been a driving force in the evolution of the planet's biodiversity.

Recognition of natural selection as a driving mechanism of evolution was the major contribution of Charles Darwin and Alfred Russel Wallace (see Chapter 2). The theory of evolution by natural selection can be stated as follows:

- Within a population, there is variation among individuals, and much of this variation is heritable, that is, due to differences among alleles.
- The environment contains limited resources, and more individuals are born than can possibly survive.
- Individuals compete for these limited resources; some individuals have characteristics that make them more likely to survive and reproduce.
- Over time, advantageous traits (alleles) are favored and disadvantageous traits are selected against, leading to an increase in the frequency of beneficial alleles and descent with modification within the population.

Given enough time, natural selection can significantly change the allele frequencies and characteristics of populations, giving rise to new species. There are three ways in which natural selection can affect the characteristics of a population. The most common way is through **directional selection** (Fig. 4.3, top), in which selection pressures move the population toward an extreme phenotype. A classic example is provided by Peter and Rosemary Grant's decades-long studies of Galápagos finches (better known as "Darwin's finches"). At this location, the climate varies year-to-year from very wet to very dry. During wet years, small seeds are plentiful, and the finches prefer these. But during dry years, the food supply shifts toward larger, tougher seeds. This provides directional selective pressure for increased frequency of larger, tougher beaks in the finch population. In **stabilizing selection** (Fig. 4.3, middle), intermediate phenotypes are favored and extreme phenotypes are selected against. Human birth weights provide an example. Babies of low birth weight tend to be unhealthy and prone to infections, and babies of high birth weight are often associated with difficult childbirths. Babies of intermediate birth weights have lower mortality rates. In **disruptive selection** (Fig. 4.3, bottom), probably the rarest type of selection, extreme phenotypes are favored and intermediate phenotypes are selected against. For example, say a population of mice varies in color, with some individuals having very dark fur, some having very light fur, and some intermediate in color. If these mice lived in an area with some patches of very dark soil and other patches of very light soil, then the dark-colored mice would be able to avoid predation by blending in with the dark colored soil, the light-colored mice would be able to blend in with the light colored soil, but the intermediate-colored mice wouldn't blend in anywhere, and so would be more susceptible to predation. Over time, this would result in selection in favor of the extreme colors, and against the intermediate coloration.

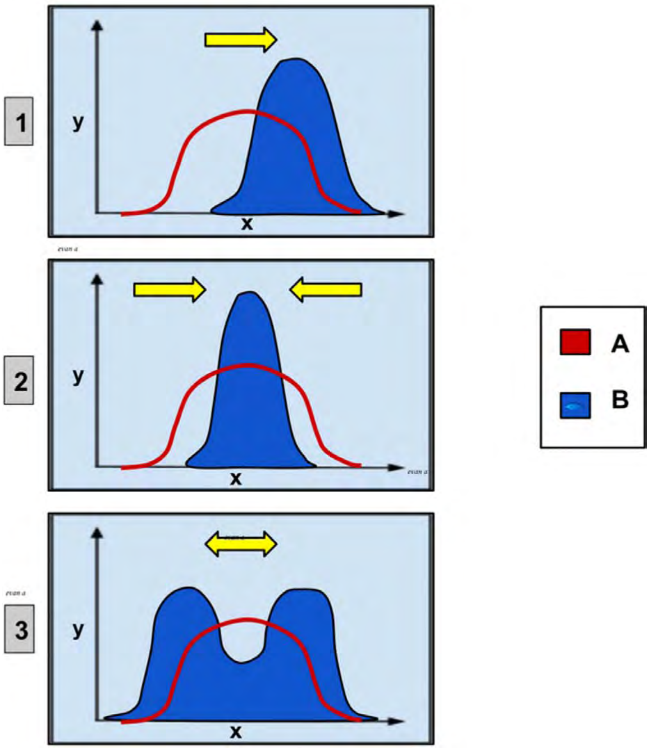

Figure 4.3: The three types of natural selection. A (red) represents the original population and B (blue) the population after selection. (Wikipedia 'Selection (biology);' Attribution: Ealbert17)

4.4 SPECIATION

For speciation to take place, populations must be isolated from each other so that little or no gene flow takes place between them, allowing the populations to diverge along their own evolutionary pathways. Eventually, enough genetic changes occur so that if the populations regain contact, they are reproductively isolated from each other. Speciation can occur as the result of several geographic scenarios. Probably the best known scenario is allopatry. In **allopatric speciation** (Fig. 4.4, left), a population is split into two or more populations that are isolated from each other through some vicariant (splitting) event, such as formation of a geographical barrier (mountain range, river valley, desert, etc.). With no gene flow among the resulting populations, the new populations diverge evolutionarily in response to environmental selective pressures, genetic drift, or both, and, given enough time, can evolve into separate species. **Peripatric speciation** (Fig. 4.4, second from left) is similar and may be considered a special case of allopatric speciation; in peripatric speciation, a small subgroup of the original population may colonize another habitat or ecological niche peripheral to the original population and, if isolated, speciation may result. In **parapatric speciation** (Fig. 4.4, second from right), a population may consist of two subpopulations with a narrow zone of overlap, perhaps due to a partial geographic barrier or some other cause. This reduced gene flow could then lead to dimorphic or behaviorally distinct subpopulations, further reducing the frequency of mating and gene flow between subpopulations, and ultimately resulting in enough evolutionary divergence for speciation to occur. Lastly, **sympatric speciation** (Fig. 4.4, right) occurs among populations that share the same geographic range. Sympatric speciation may be most common among bacteria which can undergo abrupt genetic change through horizontal gene transfer. Among multicellular organisms, sympatric speciation is probably most common among plants. This is because many plants are prone to polyploidy, or production of extra chromosome sets. This results in reproductive isolation of the polyploid population from its parent population, and potential speciation. But it is also possible that polyploidy in plants could lead to sympatric speciation among animals such as pollinating insects that have close associations with these plants. Disruptive selection (see previous section) could also theoretically lead to sympatric speciation.

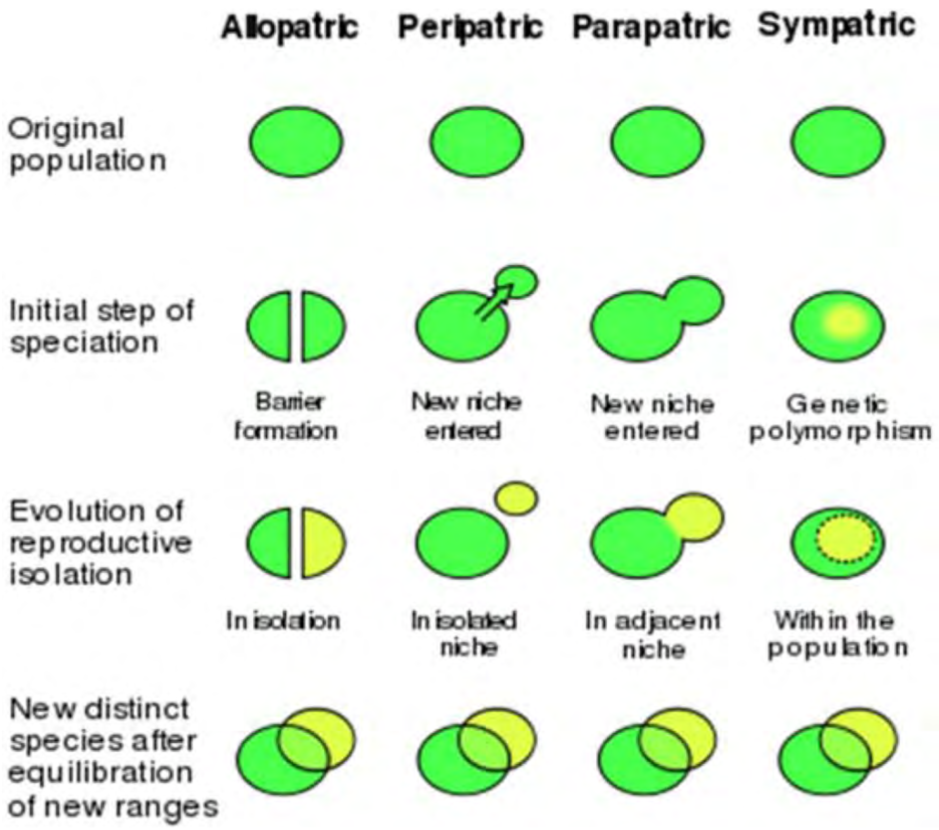

Figure 4.4: Comparison of four types of speciation (Wikipedia 'Speciation;' Attribution: Ilmari Karonen)

Based on the biological species concept, a population becomes a separate species when its members evolve traits so that they can then no longer breed with other populations and produce viable, fertile offspring. These reproductive isolating mechanisms can take several forms. **Prezygotic isolating mechanisms** prevent fertilization of the egg, and include 1) temporal isolation, in which different species are reproductively active at different times, 2) habitat isolation, in which mating is prevented because the species live in different habitats, 3) behavioral isolation, in which different species have different mating rituals, mating calls, etc., 4) mechanical isolation, in which the genitalia of different species are incompatible, or, in the case of plants, they have different pollinators, and 5) gametic isolation, in which the gametes of different species are incompatible. **Postzygotic isolating mechanisms**, which operate after fertilization, include 1) hybrid inviability (zygote does not develop or individual never reaches maturity), and 2) hybrid infertility (hybrid offspring survive to maturity but are unable to reproduce). In terms of avoidance of wasted energy (and wasted gametes), prezygotic isolating mechanisms are the most efficient. In some cases, reproductive barriers between species may involve multiple isolating mechanisms.

4.5 RECONSTRUCTING EVOLUTIONARY HISTORIES

Carolus Linnaeus gave us his system of hierarchical classification, which is still in use in modified form today. Linnaeus' original purpose was to develop a system that would allow us to categorize and organize the bewildering diversity of life on Earth, and his system still serves this important function. However, Darwin and Wallace provided us with a second important function of biological classification – to organize the world's biodiversity, past and present, based on evolutionary relationships. But, as we will see, this task is easier said than done. There have been numerous approaches to this problem, but the most widely used modern approach to biological classification is **cladistics**, or **phylogenetic systematics**, first popularized by the German entomologist Willi Hennig in the 1950s–60s. Hennig's approach is to organize taxa into "clades;" a clade is a group of taxa that includes a common ancestor and all of its descendants. But how do we achieve this? Hennig reasoned that the evolutionary history of organisms is reflected in the modifications of the characteristics of the common ancestor. If these modifications could be ordered into a sequence, then these ancestral and derived character states would provide evidence for reconstructing the evolutionary history of these related taxa, resulting in an evolutionary tree, or cladogram, of these taxa.

A clade that includes a common ancestor and all of its descendants is considered a "natural" group, and is **monophyletic** (Fig. 4.5). Monophyletic clades are constructed based on derived character states, or **apomorphies**. In particular, shared derived character states, or **synapomorphies**, are evidence of close evolutionary relatedness. **Plesiomorphies**, on the other hand, are ancestral character states retained by descendants, and do not necessarily imply close relatedness. Cladograms consisting of monophyletic clades are constructed as a series of branching events which are based on changes from plesiomorphic to apomorphic character states. Of course, it is possible, and even likely, that more than one possible cladogram can be constructed from a set of characters. In this case, cladists generally consider the most parsimonious cladogram (the one requiring the fewest evolutionary changes) to be the most likely.

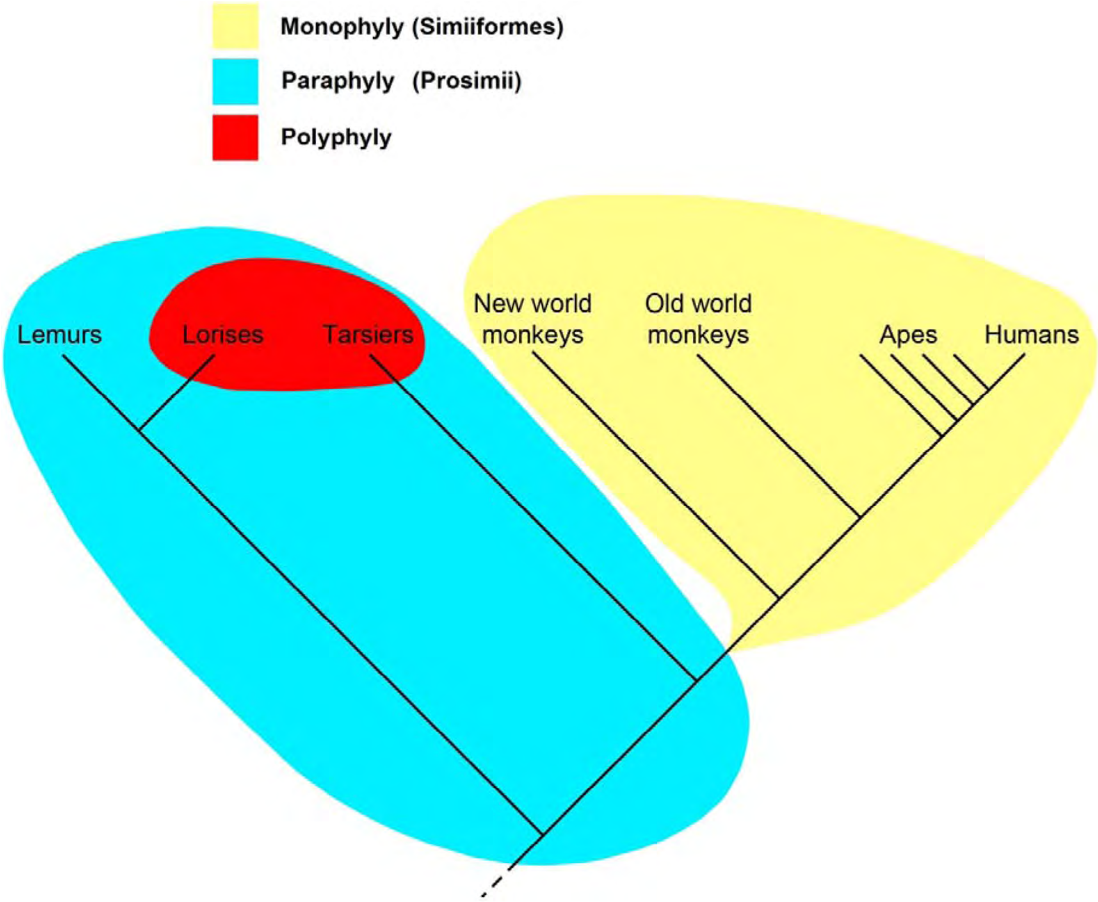

Figure 4.5: Cladogram of the primates, demonstrating the concepts of monophyly, paraphyly, and polyphyly (Wikipedia 'Cladistics;' Attribution: Original work by Petter Bøckman, revised by Peter Brown)

According to cladistics systematists, any grouping other than a monophyletic one is biologically artificial, and to be avoided. Types of groups that fall into this latter category include paraphyletic and polyphyletic groups (Fig. 4.5). A **paraphyletic** group includes a common ancestor, but excludes one or more monophyletic descendant taxa. For example, in a cladogram of the Order Primates, the taxonomic grouping Prosimii (lemurs, lorises, and tarsiers) would be paraphyletic because it would exclude the descendant clade Simiiformes (new and old world monkeys, apes, and humans), as shown in Fig. 4.5. Another example of a paraphyletic group is the traditional vertebrate class Reptilia. This class includes the common ancestor of all the amniote vertebrates (vertebrates that lay their eggs on land, or the fertilized egg is retained within the mother). However, the traditional class Reptilia excludes the birds and mammals, so it is a paraphyletic group, and therefore is considered an artificial grouping by cladists. Likewise, the group of hymenopterans commonly referred to as “wasps” would be paraphyletic if it excludes the bees and ants, which are descended from a common ancestor with the wasps. A **polyphyletic** group is even more alarming to cladists; such a group includes two or more widely separated evolutionary lineages that lead to two or more common ancestors before reaching a common ancestor. Basically, it is any taxon that cannot be called monophyletic or paraphyletic. Polyphyletic groups are often based on **homoplasies**, which are biological similarities that do not reflect recent shared common ancestry (i.e., apomorphies). Homoplasies are similarities produced by convergent evolution (the evolution of similar traits independently). For instance, as shown in the cladogram of the primates in Fig. 4.5, including lorises and tarsiers together based on night-active behavior (a trait that evolved independently in the two groups) would result in a polyphyletic grouping.

Evolution by natural selection has been a driving force generating the astounding variety of life on Earth. In the next chapter we will focus on the Earth’s biological diversity, how it is assembled, and how it can be measured.

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5 ECOLOGY, BIOMES, AND BIODIVERSITY

Your goals for this chapter are to learn about:

- The hierarchy of ecological organization
- The large-scale patterns and causes of the Earth's climatic variation
- Major biomes of the world
- Ways that biodiversity is measured
- The importance of scale in biodiversity measurement
- Taxonomic, spatial, and temporal patterns of biodiversity

5.1 INTRODUCTION

Ecology is that branch of science that focuses on relationships and interactions among organisms and their environment. As such, ecology is closely tied to evolution, since these interactions over long periods of time lead to evolutionary changes. Ecology is also intimately related to biogeography; the abundance and distribution of species are greatly affected by their interactions with each other and their physiological limits. In this chapter we will examine these interactions and some of the ways in which we can measure and quantify the diversity of the organisms involved in these interactions.

5.2 HIERARCHY OF ECOLOGICAL ORGANIZATION

In ecology, a **population** is defined as a group of actually or potentially interbreeding organisms of the same species occupying a given location at the same time. Populations exhibit the life history traits of their species, and are subject to the forces of natural selection. In the previous chapter we discussed ecological populations in the context of evolution of new species. All of the populations of different species that occupy the same area are referred to as a **community**, and a community plus the abiotic environment (air, water, temperature, humidity, minerals, etc.) is an **ecosystem**. The consistency and predictability of communities across a landscape has been greatly debated, particularly among plant ecologists of the early 20th century. **Frederic Clements** (1874–1945) viewed plant communities as relatively well-defined units, with certain species repeatedly associated with each other. Clements viewed the change over time of vegetation cover in a community as a series of successional stages, almost like the development of an organism, finally resulting in a well-defined climax community composed of coevolved species whose interactions are important in maintaining the cohesiveness of the community. Clements' views were very influential among plant ecologists, but **Henry Gleason** (1882–1975) and others challenged these views, proposing a more individualistic concept in which plant associations are more idiosyncratic and composed of a collection of species responding to their own individual requirements.

Across a landscape, a mosaic of patches forms interacting communities and ecosystems. On a more regional scale, recognizable biomes, based on the dominant plant types, are the result of prevailing climatic conditions. A **biome** is a large-scale regional community with fairly recognizable flora and fauna. The varying climatic conditions across the Earth's surface are in turn the result of many factors, including the tilt of the Earth as it rotates around the sun, large scale air and ocean currents, and topographic features of the Earth. The Earth's axial tilt remains at the same angle (about 23.4°) as it rotates around the sun. This means that, when the north pole is directed toward the sun, it is summer in the northern hemisphere and winter in the southern hemisphere, because the sun's rays are striking the Earth more directly in the northern hemisphere and more obliquely in the southern hemisphere. During those times of the year when the south pole is directed toward the sun and the north pole away, the seasons are reversed. However, because of the roughly spherical shape of the Earth, equatorial regions receive relatively consistent direct radiation from the sun throughout the year, and so these regions are consistently warm year-round.

The Earth's air circulation patterns also play a great role in shaping large-scale climatic patterns. Because the surface of the Earth is relatively warm at the equator, the warm surface air currents moving from north and south tend to rise there, forming the **intertropical convergence zone**, a low-pressure area of rising warm air. Because of the spinning of the Earth on its axis from west to east, six air circulation cells are formed, three in each hemisphere (Fig. 5.1). These cells are areas of ascending and descending air that form low and high pressure air masses. The Earth's spinning produces the Coriolis effect, a deflection in the pattern of air circulation to the right, or clockwise, in the northern hemisphere and to the left, or counterclockwise, in the southern hemisphere. The Coriolis effect, combined with the effects of the landmasses, produces a general pattern of ocean currents moving clockwise in the Northern hemisphere and counterclockwise in the southern hemisphere (Fig. 5.2).

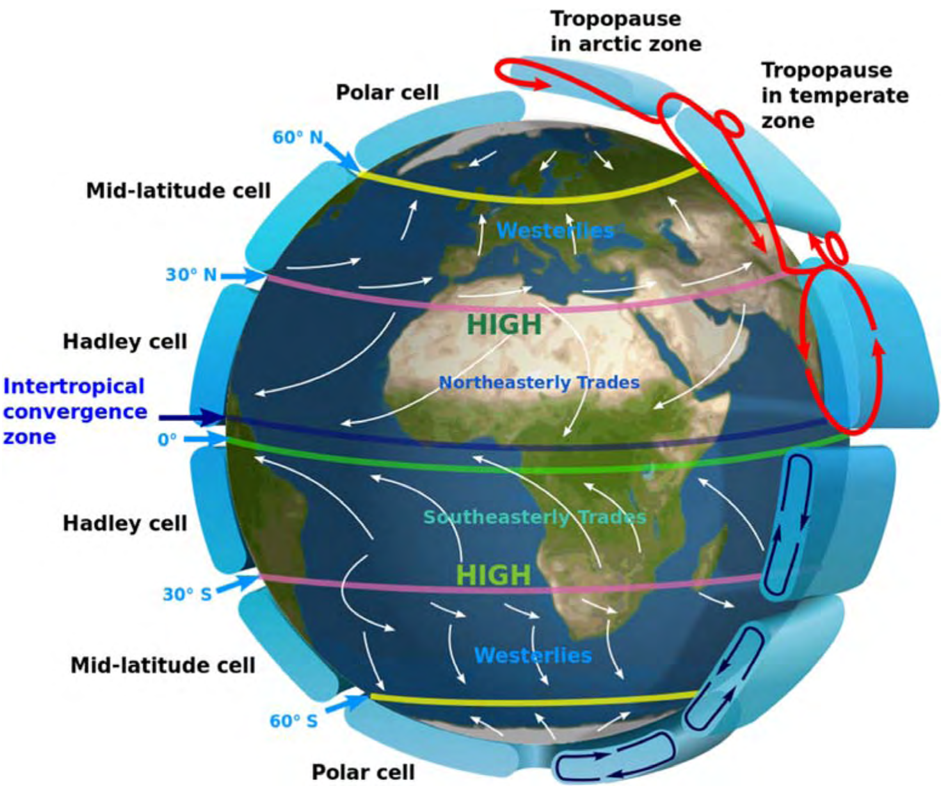


Figure 5.1: Map showing air circulation cells in relation to trade winds on the Earth's surface. (Wikipedia 'Trade Winds;' Attribution: Kaidor)

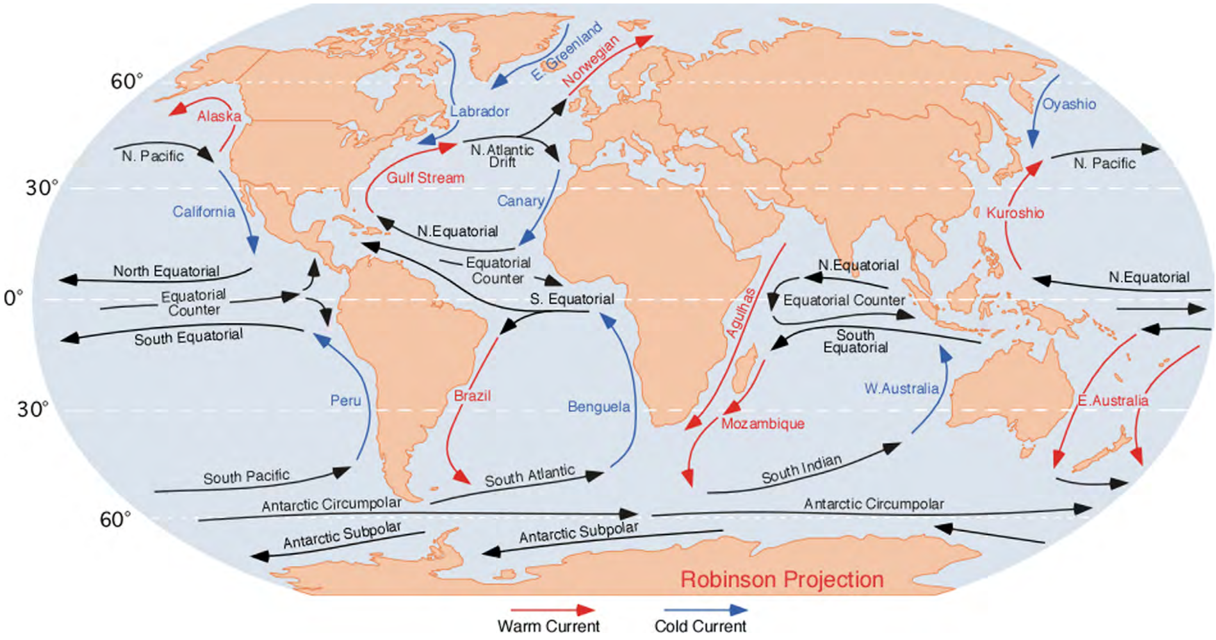


Figure 5.2: Patterns of movement of the ocean currents. (Wikipedia 'Ocean current;' Attribution: Dr. Michael Pidwirny, U.S. Government)

The combination of all of the above factors plays a great role in determining the climatic patterns we see across the Earth's surface. For instance, as the warm air of the intertropical convergence zone rises, it cools and loses its moisture in the form of rainfall. Thus, warm tropical conditions predominate in the equatorial regions. At around 30° latitude north and south, cool dry air descends to the Earth's surface, warming and taking up moisture as it does. It is around this latitude where the Earth's great deserts tend to occur. The clockwise Atlantic Ocean currents bring warm tropical waters to the east coasts of North and South America, producing moist conditions in the eastern regions of these continents; the western regions are relatively dry. The climatic patterns produced by these various factors result in large-scale regional ecological communities, or biomes.

5.3 MAJOR BIOMES OF THE WORLD

The temperature and precipitation patterns resulting from the forces discussed above in turn produce the patterns we see in the geographical distributions of the world's major biomes (Figs. 5.3). While biomes generally have recognizable and distinctive flora and fauna, there can be substantial variation in these within a biome. For instance, within the desert biome we can recognize arid and semiarid deserts, and these can vary from hot to cold deserts depending on geographic location. Another thing to keep in mind is that more local environmental factors can produce "biome-like" conditions on a smaller scale. For example, while boreal and even tundra conditions are primarily found in the far northern latitudes, these conditions can also occur at lower latitudes in high altitude mountains.

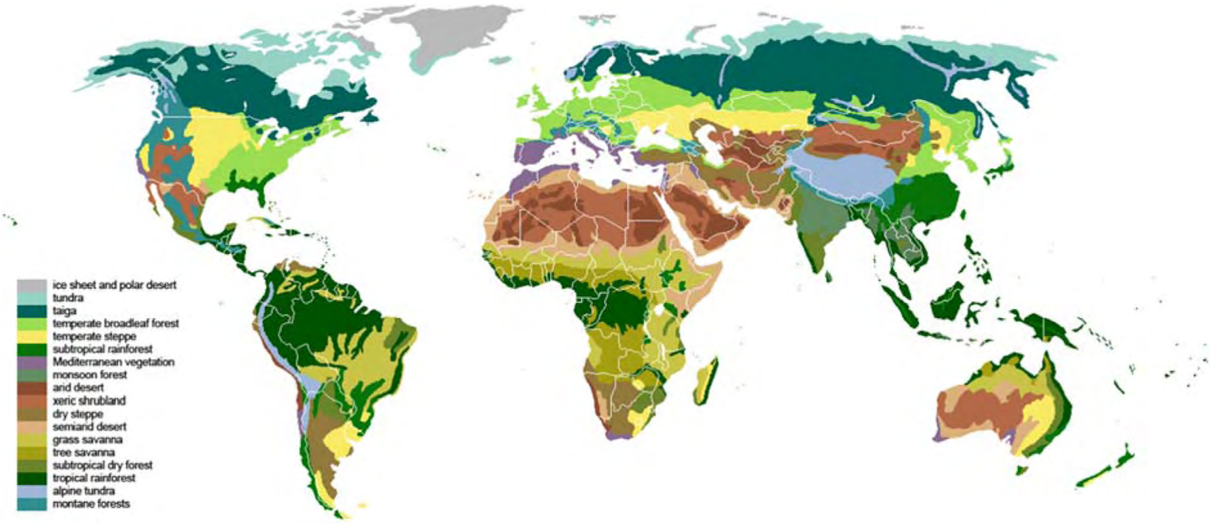


Figure 5.3: Biomes of the world. (Wikipedia 'Plant ecology;' Attribution: Sten Porse)

The world's major biomes include:

Tundra

Tundra is found primarily in the far north, above 60° latitude, but also along the Antarctic periphery and Antarctic peninsula, and at high altitudes of the world's great mountain ranges such as the Himalayas, Rockies, and Andes (Fig. 5.3). Conditions are harsh throughout most of the year in the tundra. Arctic tundra winter temperatures average below -25°C, and can dip below -50°C. Precipitation is low, less than 30 cm annually, mostly occurring in the summer. The landscape is windswept; there is little vegetation tall enough to serve as windbreaks. Tundra ground cover consists primarily of grasses and sedges, small shrubs, mosses and lichens; few if any trees are present because of lack of available water, low temperatures, and a short growing season. Permanently frozen soil, or permafrost, occurs from 25 cm or so and down, also making it virtually impossible for trees to gain a foothold. The upper soil layer undergoes alternate freezing and thawing with the seasons, resulting in a molding of the landscape into various patterned landforms. During the short summers, temperatures can reach above 10°C, producing meltwater that forms ponds and lakes across the landscape (Fig. 5.4), and allowing a short but active growing season.

Figure 5.4: Tundra in Siberia. (Wikipedia 'Tundra;' Attribution: Dr. Andreas Hugentobler)

Most plant biomass is in the roots, which are concentrated in the thawed upper soil layers. Animal life of the Arctic tundra is low in diversity, but interesting and well adapted to the harsh environmental conditions. Herbivores include large grazers such as caribou and musk oxen, as well as Arctic hares and lemmings. These animals are preyed upon by wolves, Arctic foxes, and snowy owls. Ectothermic vertebrates are absent, but some insects are found in the tundra, providing food for large numbers of waterfowl that inhabit the marshes in summer. Some of these insects turn the tables; the abundant water in the summer provides breeding sites for hordes of mosquitoes, black flies and deer flies which suck blood from the vertebrates. Terrestrial mammals are absent in the Antarctic tundra due to its isolation, but marine mammals and birds such as seals and penguins are found along the shore. Human life is sparse in the tundra, but some indigenous nomadic cultures survive in the Arctic tundra by herding reindeer and fishing.

The tundra is of intense concern ecologically because of its relationship with global warming. Melting of the permafrost would greatly disrupt tundra ecosystems. In addition, much of the Earth’s carbon is locked into tundra permafrost soils. Melting permafrost could release large amounts of the greenhouse gases carbon dioxide and methane into the atmosphere, further accelerating global warming and contributing to a dangerous positive feedback loop.

Taiga

The taiga, also known as boreal forest, is found primarily across northern North America and Eurasia, south of the tundra (Figs. 5.3, 5.5). The taiga is the world’s largest terrestrial biome. As is the case in the tundra, much of the taiga subsurface is permafrost. However, in the taiga there is enough available water and a long enough growing season to support tree growth. Tree size varies; near the tundra, trees are spaced widely apart and tree size is stunted, resulting in an open canopy. Further south, larger more dense trees produce a closed canopy. Characteristic vegetation of the taiga includes coniferous forests of spruce, fir, pine, and larch. These trees are well adapted for the cold, snowy conditions of the taiga winters. Their conical crowns and drooping limbs help in shedding snow, and biochemical changes in winter increase their resistance to freezing.

Figure 5.5: Taiga near Verkhoyansk, Russia. (Wikipedia 'Taiga;' Attribution: Becker0804)

Large herbivorous mammals of the taiga include caribou, moose, elk, and wood bison. Smaller mammals of the taiga include beaver, squirrels, voles, porcupines, and hares. A variety of mammalian predators are found in the tundra: black and brown bears, lynx, wolves, foxes, coyotes, and a diverse group of mustelids, including various weasel species, minks, and wolverines. The cold temperatures of the taiga are not conducive to high reptile and amphibian diversity, but a few species of snakes, salamanders, and frogs do live there. Several hundred species of birds have their nesting grounds in taiga; these include seedeaters such as crossbills and grosbeaks. Other bird species feed on insects that are abundant in the boggy areas. Raptors such as owls and the golden eagle prey on birds and small mammals, and ravens prey on small mammals or scavenge on animal carcasses.

The taiga supplies much of the global demand for wood and wood products, and this intense demand leads to unsustainable clear-cutting practices. During droughts, large wildfires can burn many thousands of hectares of taiga forest, but most taiga tree species are fire-adapted and regenerate well after fire if it is not too severe. The role of periodic wildfires in taiga ecology and the patterns of forest succession after wildfires are complex research questions. Adding to the complexity is the role that phytophagous forest insects play in taiga ecology. The taiga is home to a variety of damaging forest insect pests, including the spruce budworm, mountain pine beetle, spruce bark beetle, and larch sawfly. These insects can cause high tree mortality over vast areas of forest, and their impacts appear to be magnified by climate change. The complex interactions among climate change, forest insects, wildfire, and demand for wood products will play a great role in the future health of the taiga.

Temperate deciduous forest

Temperate deciduous forests, sometimes referred to as temperate seasonal forests or temperate broadleaf forests, are found in locations with warm, moist summers and cold winters, although winters are somewhat milder than those found in the previous two biomes. These forests occur primarily in the mid-latitude regions of eastern North America and across Europe and much of central Asia (Figs. 5.3, 5.6). The climates of these regions include well-defined seasonality with relatively long growing seasons. These forests are dominated by tree species such as oaks, maples, and hickories that shed their leaves each fall, resulting in the appearance and disappearance of the forest canopy seasonally. This allows deciduous trees to take advantage of the long growing season, but avoid maintenance and energy loss during the winter when conditions are not favorable for photosynthesis.

Figure 5.6: Temperate deciduous forest in northeastern Germany during leaf opening. (Wikipedia 'Temperate deciduous forest; Attribution: Dr. Hans-Peter Ende)

The thick canopy cover of mature temperate deciduous forests limits understory vegetation primarily to shade-tolerant woody species and ephemeral flowering plants that take advantage of sunlight that reaches the forest floor in the spring before the leafy canopy has developed. Much of the world's temperate deciduous forest is located in areas of uneven topography, and variation in slope, elevation, and aspect can result in dramatic differences in plant species composition. For instance, in the northern hemisphere, south-facing slopes receive more sunlight than do north-facing slopes, meaning that south-facing slopes typically have warmer, more xeric environmental conditions and correspondingly different soil conditions and flora in comparison to the cooler, more mesic north-facing slopes. Soil quality varies greatly in temperate deciduous forests, but soils in this biome are generally nutrient-rich.

Temperate deciduous forests are home to a diverse array of bird species. Many migratory birds feed on the abundant insects there. Various species of woodpeckers take advantage of the dead trees to feed on the insects and build their nests. Fallen trees and coarse woody debris provide habitat for abundant insects, reptiles, and amphibians. The southern Appalachian region of North American contains the world's greatest salamander diversity. Mammals such as squirrels and other rodents are abundant in temperate deciduous forests. Small to medium-sized predators include foxes, bobcats, and weasels, and bears are often present in larger forested areas and forest preserves.

Much of the world's temperate deciduous forests has been destroyed and fragmented due to human activities. Historically, colonizing humans have harvested trees for timber, firewood, and potash, a component of fertilizer. High grading (selective harvesting for the highest quality timber) has often been practiced as well. This means the remaining trees are generally of poor genetic quality, resulting in a gradual decrease in stand quality over time. Because of the high quality soils, large areas of temperate deciduous forest have also been cleared for agricultural uses. Of course, the reduction of temperate deciduous forests to small fragments has had dramatic effects on animal life. Historically, large predators such as wolves and cougars roamed the forests. But these animals require larger areas of habitat than most forest fragments provide. In the absence of these predators, prey species such as deer often become overpopulated, and their feeding activities can have adverse effects on herbaceous vegetation and tree regeneration.

Temperate grassland

Temperate grasslands (Figs. 5.3, 5.7), also known as temperate steppes or pampas, are found in regions with warm summers and cold winters, but with less precipitation than is found in the temperate deciduous forest. Soils are generally deep and nutrient-rich, but there is not enough precipitation to support much tree growth. Periodic fire plays an essential role in maintaining many grassland environments by preventing establishment of invasive plant species and by releasing nutrients back to the soil. The largest areas of temperate grassland occur in central North America, where it is referred to as "prairie," central Eurasia ("steppes"), and east-central Argentina, Uruguay, and southernmost Brazil ("pampas"). In North America, precipitation declines from east to west, and the grasslands display a gradient of tallgrass prairie in the eastern part of the grassland range, to mixed-grass prairie in the Great Plains, and then shortgrass prairie further west, grading into the subtropical and cold deserts of the southwest and Great Basin, in the rain shadow of the Rocky Mountains. In general, conditions in the steppes are cold and dry, and shortgrass species predominate, whereas in the moister tropical air of the pampas, tallgrass species are more dominant. But both regions also show variation and gradients of vegetation based on water availability.

Figure 5.7: The Konza tallgrass prairie in the Flint Hills of northeastern Kansas, USA. A small herd of bison is in the background. (Wikipedia 'Grassland;' Source unknown)

Before the arrival of Euro-Americans, the North American prairies were home to vast herds of large grazing ungulates, namely bison and pronghorns. But in the 1800s, these numbers declined precipitously, primarily due to overhunting. By the end of the century there were only a few hundred bison left in the U.S. Bison are ecologically important in North American temperate grasslands. Their activities play a great role in shaping the prairie ecosystems. By selectively feeding on the dominant grasses, bison increase prairie plant diversity by allowing forbs to thrive. Bison feeding also increases photosynthesis rates by increasing light availability. Bison increase habitat quality for prairie dogs, which in turn provide food for numerous predators. And of course bison were of critical importance to the survival of Native American plains cultures. Overhunting by Europeans decimated bison populations, which contributed to the decline of the Native American plains tribes and decreased the quality of prairie ecosystems. Subsequent destruction of these grasslands for the purpose of agriculture and other human activities has left less than 2% of the original prairie intact. Reconstruction of grassland ecosystems is an important and challenging focus in the field of restoration ecology.

Tropical savanna

Tropical savannas (Figs. 5.3, 5.8) are located in regions with consistently warm climates that have highly seasonal rainfall patterns that can vary greatly from year to year. Such conditions are found in large swaths of northern and central South America, central and southern Africa, and much of India and Australia. Most savannas occur in locations with little topographical relief and relatively poor soils. Typically, savannas have primarily grassy ground cover, with scattered woody shrubs or trees such as acacias or eucalyptus, that do not form a closed canopy. However, substantial variation exists; the abundance of woody vegetation is determined primarily by moisture availability, which is a function of rainfall and soil characteristics. Areas with greater amounts of available moisture tend to have more dense woody vegetation. Savanna vegetation is well adapted to the frequent fires that occur during the dry season and that suppress the establishment of most tree seedlings.

Figure 5.8: Acacia savanna, Taita Hills Wildlife Sanctuary, Kenya.
(Wikipedia 'Savanna;' Attribution: Christopher T. Cooper)

Savannas support a high abundance and diversity of herbivores. The African savannas in particular are known for their huge numbers and diversity of vertebrate grazers and browsers, including zebras, giraffes, wildebeests, and many species of antelopes; some of these herbivores migrate seasonally, following the green vegetation. Elephants play an important role through their feeding on shrubs and trees, which promotes growth of grasses by reducing canopy cover and competition for water and nutrients. Lions, cheetahs, hyenas, and jackals prey or scavenge on the diverse savanna herbivore fauna. Insects are also important components of the savanna ecosystem. Grasshoppers feed on the vegetation, dung beetles are associated with the dung of the large herbivores, and termites build large mounds and underground galleries, mixing and enriching the soil in the process.

Much of the world's savanna has been dramatically altered by grazing of livestock. Overgrazing reduces the abundance of grasses competing for water, resulting in more water for woody vegetation and increased establishment and growth of these woody plants. Furthermore, the amount of fuel available for fires is decreased, resulting in less frequent and cooler fires, which also means less suppression of woody shrub and tree establishment. These factors are resulting in encroachment by woody vegetation and reduction of savannas in many locations. Livestock grazing can also reduce the savanna grass cover to the point that desertification takes place; this is a common occurrence in locations near the Sahara desert, and may have been partially responsible for the expansion of the Sahara over the last few thousand years.

Desert

The major deserts (Figs. 5.3, 5.9) of the world are located where atmospheric air circulation patterns, rain shadows, or isolation from moist ocean air results in arid conditions, typically with less than 20 cm of precipitation per year. Much of the world's hot tropical deserts are located near 30° latitude north and south, known as the "horse latitudes." It is around this latitude where air from the Intertropical Convergence Zone descends, forming a high pressure zone with little precipitation (Fig. 5.1). However, not all deserts are hot; deserts are defined by lack of moisture rather than high temperatures. Cold deserts are generally found at higher latitudes, and are the result of rain shadow effects. The Great Basin Desert of the western United States and the Gobi Desert of China and Mongolia are cold deserts formed by rain shadows associated with the Sierra Nevada and Himalaya Mountains, respectively. These deserts have high summer temperatures, but winter temperatures can drop to well below freezing. Temperatures in the Gobi Desert, for instance, can range from -40°C to 50°C.

Figure 5.9: Cacti in the Baja California Desert, Mexico. (Wikipedia 'Desert;' Attribution: Tomas Castelazo)

As indicated above, the desert biome displays a great deal of variation, not only in temperature, but in type and amount of vegetation and the animal life that it supports. Hot deserts, such as the Sahara, Arabian, and Chihuahuan, contain plants with a variety of adaptations for persisting in those extreme environments. In North America, these include such species as creosote bush and deep-rooted plants like mesquite, with taproots that can reach the water table. Succulents such as various species of cacti are also common; they can store water in their stems, and have shallow but extensive root systems that quickly take up water that becomes available during the infrequent rainfalls. The Sahara desert of North Africa covers a vast area of over 9 million km^2. It is home to almost 3000 species of plants, including many endemics.

Prominent animals of North American hot deserts include coyotes, pronghorn, roadrunners, rattlesnakes, kit foxes, mule deer, horned lizards, and desert tortoises. The Sahara is home to various species of gazelles and antelope, fennec foxes, cheetahs, monitor lizards, vipers, and scorpions. Cold deserts are often dominated by shrubby vegetation such as sagebrush (*Artemisia* sp.) and halophile (saline soil-tolerant) chenopod plants such as *Atriplex* sp. and the Australian genus *Maireana*. Depending on geographic location, prominent animals of the cold deserts include camels, gazelles, polecats, and plovers in Asia, and coyotes, mule deer, pronghorn and jackrabbits in North America.

Although rugged in appearance, in reality desert ecosystems are easily damaged. Mining, off-road vehicles and military exercises can cause serious damage to the fragile desert ground cover. Grazing along the desert margins can cause extensive degradation as well. In many locations, intensive irrigation has been used to convert desert ecosystems into agricultural land. Perhaps the greatest threat to the world's deserts is climate change. Warmer temperatures could increase frequency and intensity of wildfires, which would have a dramatic effect on desert plant biodiversity, and changing rainfall patterns would disrupt many desert ecosystems as well. Conversely, some deserts, such as the Gobi and Sahara, are actually increasing in area, as human activities such as deforestation, overgrazing, and water depletion in adjacent semi-arid lands cause desertification.

Shrubland

The world's major shrublands are found in five regions that have a Mediterranean climate – hot, dry summers and cool, moist winters. These five regions include the chaparral (Figs. 5.3, 5.10) of southern California and the Baja peninsula of Mexico, the central Chilean matorral, the regions bordering the Mediterranean Sea, the cape region of South Africa ("fynbos"), and southern and southwestern Australia ("kwongan"). These disparate locations are characterized by sandy soils and shrubs and small trees with thick bark and small, evergreen leaves.

Figure 5.10: Chaparral, Santa Ynez Mountains, near Santa Barbara in southwestern California, USA. (Wikipedia 'Chaparral;' Attribution: Antandrus)

A "shrub" is difficult to define, but is generally considered to be a highly branched, often multi-stemmed woody plant less than 8 m high. The shrubland biome is dominated by sclerophyllous ("hard-leaved") shrubs; the small, leathery evergreen leaves with their thick cuticles are well adapted for conservation of moisture during the dry summers that characterize this biome. Some prominent plants of the shrubland biome include scrub oak and chamise in California, king protea and pincushions in South Africa, and *Kingia australis* and tinsel lilies in southern Australia. The shrubland biome is prone to infrequent periodic fires because of the dry summers and the profusion of dry, woody fuel. Consequently, plants of the shrubland biome tend to be fire-adapted, resprouting or producing seeds that germinate in response to heat from a fire. It has been estimated that the shrubland biome contains roughly 20% of the world's plant species, including many endemic species. Animal life in the shrubland biome includes mule deer, jackrabbits, coyotes, pinyon mouse and western scrub jay in California, and kangaroos, wallabies, honey possums, and southwestern pygmy possums in Australia.

Because of the large number of endemic species, shrubland environments are of great conservation concern. This is especially true in Australia, where the kwongan is the country's only recognized global biodiversity hotspot. Threats to this environment include land clearing, climate change, and invasive species, especially *Phytophthora cinnamomi*, an invasive soil-borne water mold that causes root rot, known there as phytophthora dieback. Plants in several genera are susceptible, and a decline in these plants could also adversely affect nectarivorous animals, such as the honey possum and southwestern pygmy possum mentioned above, that depend on these plants.

Tropical forest

Tropical forests are found primarily in the equatorial regions of the world, generally where annual rainfall exceeds 200 cm and temperatures are consistently high, with annual temperature above 24°C (Figs. 5.3, 5.11). The largest expanse of tropical forest is in the Amazon basin, but there are also substantial areas of tropical forest in other Neotropical regions, Africa, Southeast Asia, and the Indonesian region. As is the case with other biomes, there is substantial environmental variation within the general tropical forest biome. The classic rainforest (Fig. 5.11) environment generally occurs in lowland regions, where rainfall and temperature are consistently high. But the tropical forest biome also includes seasonal tropical forests, with a well-defined dry season in which many plant species shed their leaves, and montane tropical forests, often referred to as cloud forests, which occur at higher elevations with cooler climates.

Figure 5.11: Daintree Rainforest, Queensland, Australia.
(Wikipedia 'Tropical rainforest;' Attribution: Thomas Schoch)

Tropical forests contain the world's greatest diversity of terrestrial organisms. Over half of all known species of plants and animals live within the 6% of the world's land surface that is tropical forest, with the greatest diversity in the rainforests. One reason for this great diversity is the characteristic vertical stratification of tropical rainforests. Well-defined ground, understory, canopy, and emergent tree strata provide abundant ecological niches for a huge variety of organisms. Lianas (climbing vines) and epiphytes (plants that live on the surface of other plants) take advantage of the vertical structure provided by the dense tree growth. The warm, wet conditions of the tropical rainforests support high plant productivity and high rates of decomposition. Plant litter is decomposed rapidly, releasing nutrients which are quickly taken up by the plants. This explains why rainforest soils are often relatively nutrient-poor, but can still support high primary productivity. The diversity of plant species and structure provide homes and resources for many species of vertebrates, as well as countless species of insects and other invertebrates. The montane and seasonal tropical forests contain somewhat lower diversity, but many endemic species, and include some of the world's most endangered ecosystems.

Tropical forests are disappearing at an alarming rate. Traditionally, subsistence farmers have practiced Swidden, or "slash-and-burn" agriculture, in which relatively small plots of forest are cut down and burned. This clears the land for planting, but also returns some of the nutrients to the soil in the form of ash. The land is then farmed for a few years, but crop yields decline over time because of nutrient depletion. Eventually, the land is abandoned and left fallow, and the farmers move on to clear another plot of forest. Given enough time, soil nutrient levels generally recover after abandonment, so Swidden agriculture can be a sustainable form of agriculture at low human population levels. However, when population levels are too high, which is the case in many tropical regions, then land use becomes too intense, fallow periods aren't long enough, and over time the landscape becomes degraded and unproductive.

Large scale deforestation related to logging, cattle grazing, and agriculture to meet global demands for these products is of much greater ecological concern. Currently, a major impetus to destruction of tropical forests in many locations is global demand for palm oil, which is leading to massive clearing of forests for palm plantations. Loss of tropical forests is of great concern because of the potential catastrophic loss in biodiversity; it has been estimated that up to 50,000 species per year are doomed to extinction because of tropical deforestation. In addition to the high biodiversity they contain, tropical forests play a critical role in carbon sequestration, and decline of these forests will result in an increase in the greenhouse gas CO_2 in the atmosphere.

Anthropogenic biomes

The above biomes describe major vegetation types that occur across the Earth's surface primarily as a result of global climate patterns. These biomes represent patterns that we would expect in a "natural," undisturbed state. However, as we have noted, humans have fundamentally altered much of the Earth's surface. In 1700, about half of the terrestrial biosphere was unaltered by human activities, but by 2000 only about ¼ was left unaltered. The concept of "anthropogenic biomes," or "anthromes," has been developed to reflect this reality. Anthropogenic biomes include urban settlements, villages, croplands, rangelands, and semi-natural lands. This concept allows us to view the interactive nature of human activities with the Earth's ecological systems, and may provide greater insight into ways that humans can exist within the natural world in a sustainable manner.

5.4 PATTERNS IN THE EARTH'S BIODIVERSITY

In this section we will examine geographic and temporal patterns in the world's biological diversity, or "biodiversity." But before proceeding further with a discussion of biodiversity, it would be helpful to take a closer look at what we mean by the term "biodiversity," and some of the ways in which biodiversity is measured. In the broad sense, biodiversity refers to the variety of life on Earth. This can include variation at many different levels ranging from genetic to landscape or even biome-level biodiversity. Most studies of biodiversity focus on the species level, and the most common measure of biodiversity is species richness. **Species richness** is the number of species present in a given geographic area, and is probably the simplest and most straightforward measure of biodiversity. But species richness only tells part of the biodiversity story, for a simple count of the number of species present doesn't take into account how evenly represented the different species are; in other words, how close to each other in abundance the species are. For instance, a community with 10 species in which 1 of those species contains 90% of all the individuals in the community has the same species richness as another community with 10 species in which each species has roughly the same number of individuals. But the second community is intuitively more diverse.

There are several diversity indices that incorporate both richness and evenness; one of the most popular is the **Gini-Simpson index**, often just referred to as the Simpson index in ecological work, although there are several related indices that are also referred to as "Simpson index," so caution should be taken. The Gini-Simpson index produces a value ranging from 0 to 1, which represents the probability of two randomly selected individuals from the community being different species. Smaller values represent lower diversity and larger values higher diversity. But again, these diversity indices are oversimplifications of reality, because they treat all species the same, without considering the ecological roles and different evolutionary histories of the various species.

Two other approaches to measuring diversity are trait diversity and phylogenetic diversity. **Trait diversity** measures the diversity of (generally morphological) features in a community, with the reasoning that high trait diversity reflects high diversity of ecological roles. For example, a community with 10 bee species having a variety of different tongue lengths would have higher trait diversity than one with 10 species having similar tongue lengths, reflecting a greater variety of flower visitation habits (flowers with different tube lengths) among the bees in the first community. **Phylogenetic diversity** takes into account the evolutionary distances between species comprising a community; intuitively, a community of species that is more varied phylogenetically is more diverse. For instance, a community with 10 pollinating insect species, all of which are bees, would have less phylogenetic diversity than one with10 pollinating species that included 3 butterfly, 2 beetle, 4 bee, and 1 fly species.

When doing a species inventory at a particular location, methodological limitations must be taken into account. For relatively stationary species such as plants and many soil invertebrates, sampling within well-defined plots can provide good estimates of diversity. However, for motile animals such as most vertebrates and insects, diversity estimates are more difficult, and some sort of trapping method is often necessary. Any trapping method will have inherent biases; some species will be more or less likely to be collected by a given trap type. If possible, a variety of sampling methods should be used to give a more complete picture of the species diversity present.

A related question in regard to sampling for biodiversity is: "how do we know how complete our species inventory is?" We know how many species our sampling program collected, but can we estimate how many species are remaining that we haven't collected? One approach to answering this question is to construct a species accumulation curve. The cumulative number of species discovered is plotted as a function of sampling effort, such as number of traps used or person-hours spent collecting. With increasing effort and species accumulated, the curve will increase, but at a progressively lower rate. Eventually, if the inventory is relatively complete, the curve will approach its asymptote (meaning few or no new species are being collected), providing an estimate of the total number of species (collected and not collected combined) present. Other useful methods for estimating minimum species richness have been developed by Anne Chao and colleagues; these estimates are based on the number of rare species collected, and are described in their 2009 paper in the journal *Ecology*.

The scale at which biodiversity is measured is also an important consideration. Ecologists generally recognize three levels of diversity within a landscape; alpha, beta, and gamma diversity. **Alpha diversity** is local diversity; diversity within a defined unit, such as a community or habitat. But across a landscape, the alpha diversities of these units will probably vary to some extent. The extent of the variation in the alpha diversities is known as **beta diversity**. **Gamma diversity** represents the overall diversity of the entire landscape. In biodiversity studies, it is of critical importance to be aware of the scale at which diversity is being measured.

It is also important to remember that biodiversity can and does change over time, often in a predictable manner, such as in the successional change from field to forest. There is evidence that frequency of disturbance affects diversity. The **intermediate disturbance hypothesis** suggests that, in many communities, intermediate frequencies of disturbance actually maximize biodiversity by allowing some colonization to persist in the community. Very frequent disturbances restrict biodiversity to early colonizing species at the expense of later successional species, but very infrequent disturbance allows later successional species to outcompete earlier successional species, reducing diversity.

Conservation of the Earth's biodiversity is of paramount importance. To assess the rate and causes of biodiversity loss, we need to know how much biodiversity there is, and how it is distributed, not only geographically, but taxonomically. The unfortunate fact is that we still have relatively little detailed knowledge of much of this biodiversity, but broad patterns are apparent. To begin with, most of the world's biodiversity is represented by the smaller organisms. To cite one example, one order of insects, Coleoptera (the beetles), contains over 300,000 known species. This is more than six times the number of all known vertebrate species. But even this number falls well short of the number of predicted species, and estimates ranging up to 80 million have been proposed for the Arthropoda, the animal phylum that includes the insects. Among the eukaryotes, most of the world's vertebrates and vascular plants have probably been cataloged. But groups such as the insects and other arthropods, nematodes, protozoa, algae, and fungi have undoubtedly had only a small proportion of their diversity cataloged, and there is even more to be learned regarding prokaryote diversity.

The Earth's biodiversity is the result of evolutionary processes that have been at work for some 3.5 billion years. For most of that period, life was restricted to prokaryotes and single-celled eukaryotes. The Cambrian explosion, during which almost all phyla of multicellular organisms appeared, marked the beginning of the Phanerozoic Eon 540 million years ago. Since then, the history of the Earth's biodiversity has been punctuated by five mass extinctions as well as several smaller ones, as shown in the graph of marine fossil diversity in Fig. 5.12. The last 200 million years have seen a consistent increase in biodiversity in the fossil record; there is debate among paleontologists as to whether this is an artifact of a more complete and better preserved recent fossil record compared to that of earlier strata, or if it represents an accurate picture of temporal changes in biodiversity.

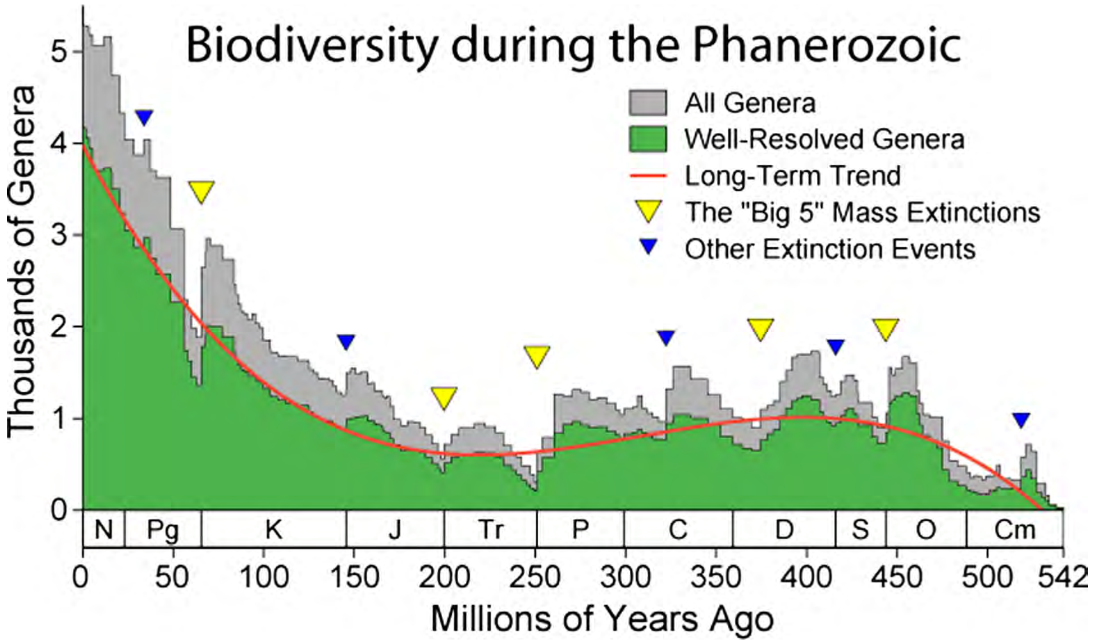
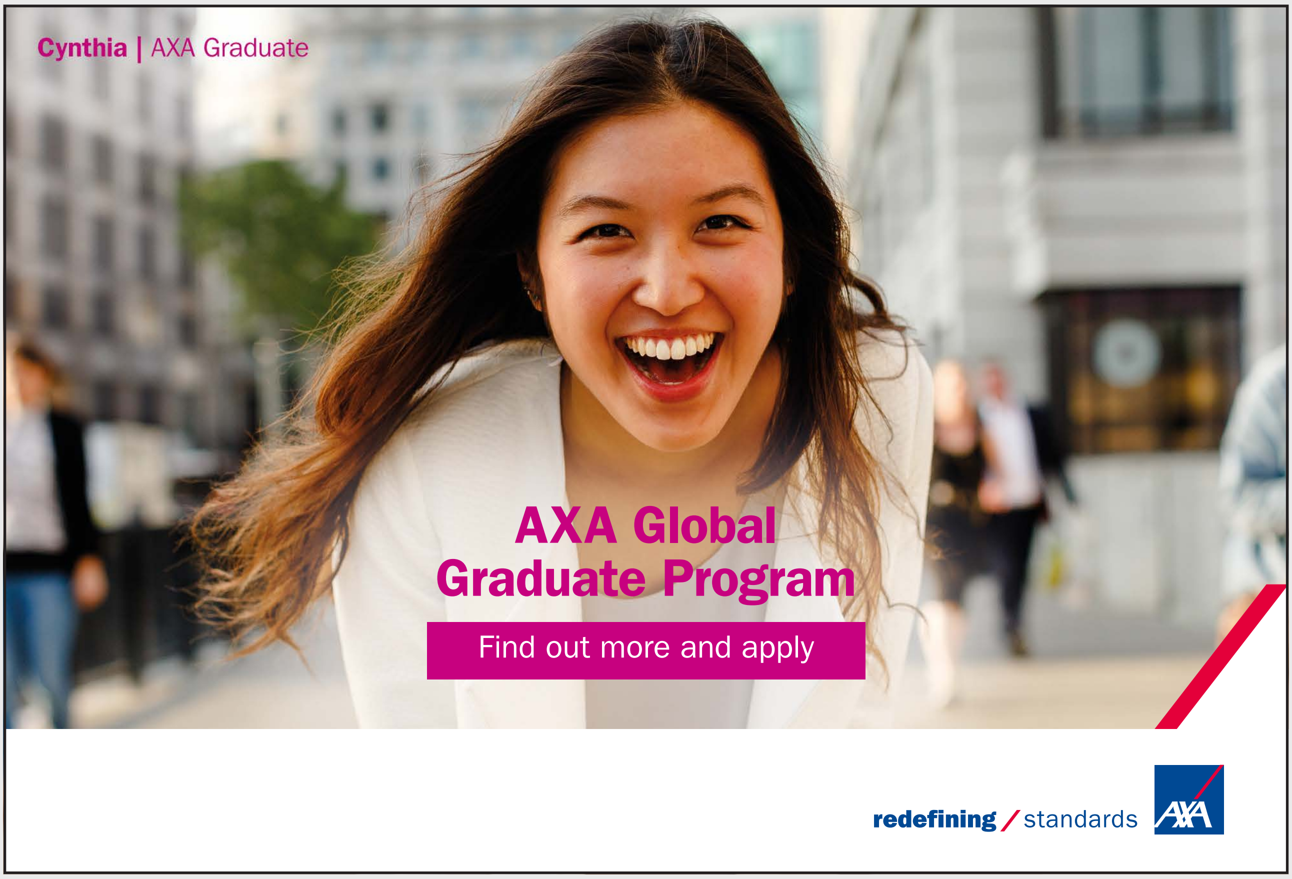


Figure 5.12: Apparent marine fossil diversity during the Phanerozoic Eon. Note that the time line (x-axis) moves from most recent (left) to less recent (right). (Wikipedia 'Biodiversity;' Attribution: Dragons flight)

With regard to current biodiversity, a striking spatial pattern emerges, which we have already noted – the high biodiversity of the equatorial regions, in particular the rainforests. There is a general trend of increasing biodiversity from the higher latitudes to the equator. There has been much debate among biogeographers regarding the causes of this pattern, and many hypotheses have been proposed. Some biogeographers have suggested that the greater rates of photosynthesis and primary production at lower latitudes support higher population levels and thus decreased extinction rates. Another leading hypothesis revolves around rates of evolution and time since large-scale environmental perturbation. Based on this latter view, lower latitudes would be expected to have greater biodiversity because (1) the warmer climate leads to faster mutation rates and rates of evolution, and (2) the equatorial regions largely escaped the dramatic reduction in biodiversity suffered by higher latitudes during glaciation; therefore, populations in the lower latitudes have had longer to evolve, or conversely, populations in higher latitudes haven't had enough time to "catch-up." There are other hypotheses as well, and explaining the latitudinal gradient in species diversity is still an important focus in biogeography.



To identify regions of great biodiversity importance and to prioritize conservation efforts, global "biodiversity hotspots" have been identified. The concept was first developed by conservation biologist Norman Myers, who identified 25 areas (shown in green in Fig. 5.13) around the world that met two criteria. A biodiversity hotspot (1) must have at least 0.5% or 1,500 of its species of vascular plants considered endemics, and (2) must have lost at least 70% of its vegetation. Since Myers work, 9 more locations have been added (shown in blue in Fig. 5.13). Relatively little of the total area within these biodiversity hotspots is protected, and recognition of these areas as important in biodiversity conservation has led to increased efforts to protect them. On the other hand, the concept of biodiversity hotspots has received criticism for several perceived shortcomings, including lack of attention to other (non-vascular plant) taxa, too much emphasis on past, rather than present, habitat loss, and too much focus on species richness rather than other, possibly more meaningful measures of diversity.

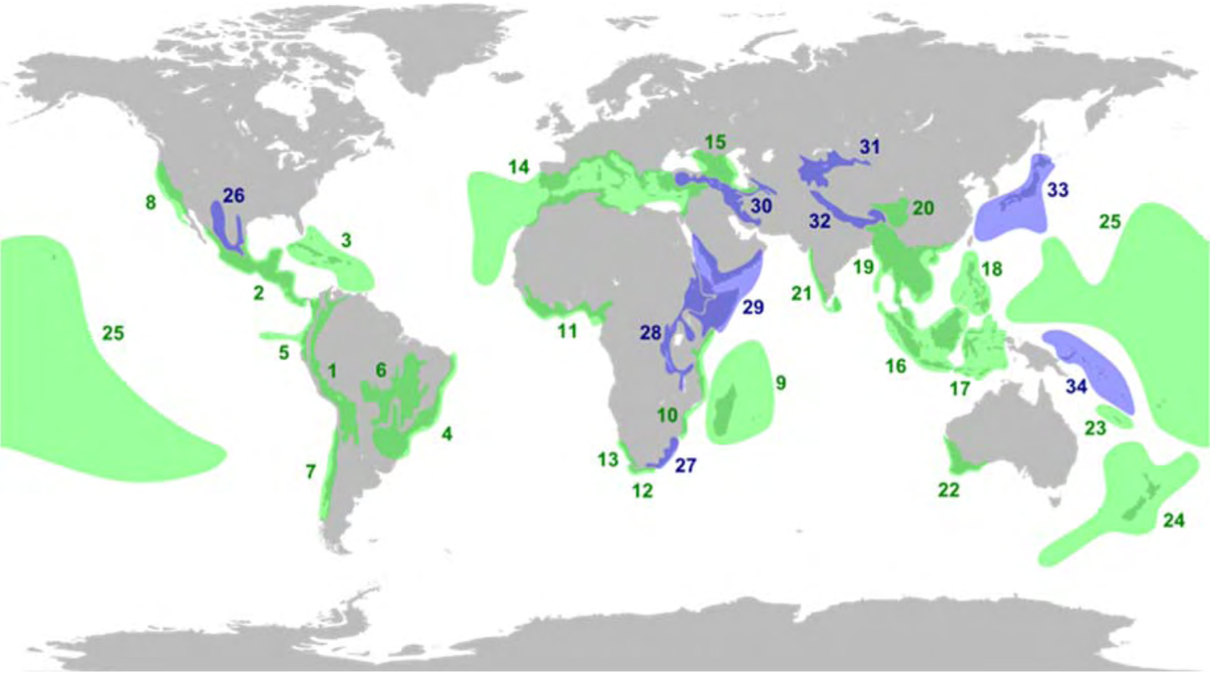


Figure 5.13: Biodiversity hotspots. Original regions in green, added regions in blue. (Wikipedia 'Biodiversity hotspot;' Attribution: World_map_blank_without_borders.svg)

One of the most fascinating and important areas of biogeography has involved efforts to explain patterns of biodiversity and the causes of these patterns. The field of island biogeography has been at the forefront of these efforts, and has made important theoretical contributions as well as laying the groundwork for applications in conservation biology. We will consider the biogeography of islands and oceans in the next chapter.

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6 ISLANDS AND OCEANS

Your goals for this chapter are to learn about:

- How islands form
- Hazards and advantages of island life
- The "island rule"
- Factors affecting species richness on islands
- Differences between marine and terrestrial environments and organisms
- Marine biogeographic realms and pelagic zones
- Ocean trenches, ridges, and hydrothermal vents
- Coral reefs

6.1 INTRODUCTION

Island life has always fascinated biogeographers. Many islands are isolated from potential sources of immigrants, meaning that the biota of islands follow their own evolutionary pathways that often diverge dramatically from mainland relatives. We see this pattern in the unique flora and fauna of the island continent of Australia, as well as South America until formation of the Panama land bridge. Evolutionary patterns are often magnified on islands, and island biogeography has played a central role in the development of evolutionary theory. Charles Darwin was an island biogeographer; Galápagos (Fig. 6.1) island life provided impetus for Darwin's theory of evolution by natural selection. The same was true of Alfred Russel Wallace and his work on the Indonesian islands. Islands continue to provide excellent opportunities for natural experimental studies, since they are often relatively simple ecosystems with well-defined boundaries. In this chapter, we will examine patterns of diversity on islands.

Figure 6.1: A satellite image of the Galápagos Islands (overlaid with names of major islands), about 900 km west of continental Ecuador. (Wikipedia 'Galápagos Islands;' Attribution: U.S. National Oceanic and Atmospheric Administration)

6.2 ISLAND FORMATION

There are several different types of oceanic islands, based on the processes that lead to their formation. Continental islands are part of the continental shelf, but are separated from the mainland by water, or have become separated from the mainland by seafloor spreading. The Indonesian Islands of Borneo, Sumatra, and Java are continental islands, as is New Zealand. Another type of island is the volcanic island arc, in which the movement of one subduction plate under another produces geological uplift that result in island formation. The Aleutian Islands, extending from the Alaska Peninsula to the Kamchatka Peninsula of Russia, exemplify this island type. A third island type forms as the result of volcanic hotspots, which are thought to be hot mantle plumes that form volcanoes. Generally, these are chains of islands that form sequentially as the oceanic tectonic plate moves over the hotspot. As the recently formed island moves away from the hotspot, another is formed from the seafloor that now lies over the hotspot; over millions of years, an island chain forms, with the youngest (volcanic) one at the hotspot and the oldest one at the opposite end of the chain, and perhaps submerged. The Hawaiian Islands and the Galápagos Islands formed via this process.

6.3 GETTING THERE AND SURVIVING THERE

Seawater is not a friendly environment for most terrestrial organisms, so most organisms that colonize oceanic islands must disperse across the ocean barrier rather than surviving in it. Animals that are strong fliers, such as large birds and bats, can reach isolated islands under their own power, and some insects and smaller flying vertebrates may be aided by strong winds. Occasionally, small nonflying animals that otherwise could not disperse to a distant island may arrive there via transport via masses of floating debris. Some plants have floating seeds or fruits that can be carried by ocean currents to isolated islands; the coconut palm is an example. Other plants have very light or winged seeds that can be borne by the wind, and of course some have seeds with hooks or adhesive substances that allow them to hitch a ride on animals. As you might expect, islands, and particularly isolated islands, tend to have biotas that are largely composed of descendants of good dispersers. Nevertheless, long-distance dispersal by terrestrial vertebrates has been documented, including distances of hundreds of miles by various reptiles, amphibians, and mammals. Even elephants can swim up to 48 km based on estimates. Once there, species with broad feeding niches seem to be at an advantage, which makes sense; food might be scarce, and a specialist feeder could have difficulty finding its required food. In general, herbivorous colonizers fare better than carnivores, and smaller animals, which require fewer resources, are more successful than large ones. Asexual reproduction and self-fertilization capabilities are also advantageous, for obvious reasons, in a newly colonized location.

Organisms that inhabit islands face a variety of hazards. Island populations are generally smaller than those on large landmasses. Small population size means an increased likelihood of extinction. For instance, while islands account for only 20% of bird species and subspecies, 90% of bird extinctions since 1600 have been island birds. Small populations also mean low genetic diversity, making island populations less capable of evolving resistance to introduced pathogens, and on small islands there may be no refugia to allow escape from introduced natural enemies. Island animals are often slow-moving and "naïve" with regard to introduced predators, and many island bird and insect species are flightless, which often makes them virtually defenseless against these introduced marauders. These island species are often at a competitive disadvantage as well. Exacerbating the above dangers is the fact that islands are often ecologically and climatically unstable. However, there are advantages for those species that successfully colonize islands. Island colonizers often leave behind their mainland predators and pathogens, and have fewer natural enemies in their new island home. Ecological niches with little competition may be available. The availability of new ecological niches on islands has led to many examples of dramatic adaptive radiations, such as Darwin's famous Galápagos finches, and the honeycreepers of Hawaii (Fig. 6.2). The latter birds are descended from an ancestral finch-like colonizer, and their adaptive radiation has produced 11 endemic genera and many species, with beaks that reflect adaptations to a variety of feeding niches (Fig. 6.2, right).

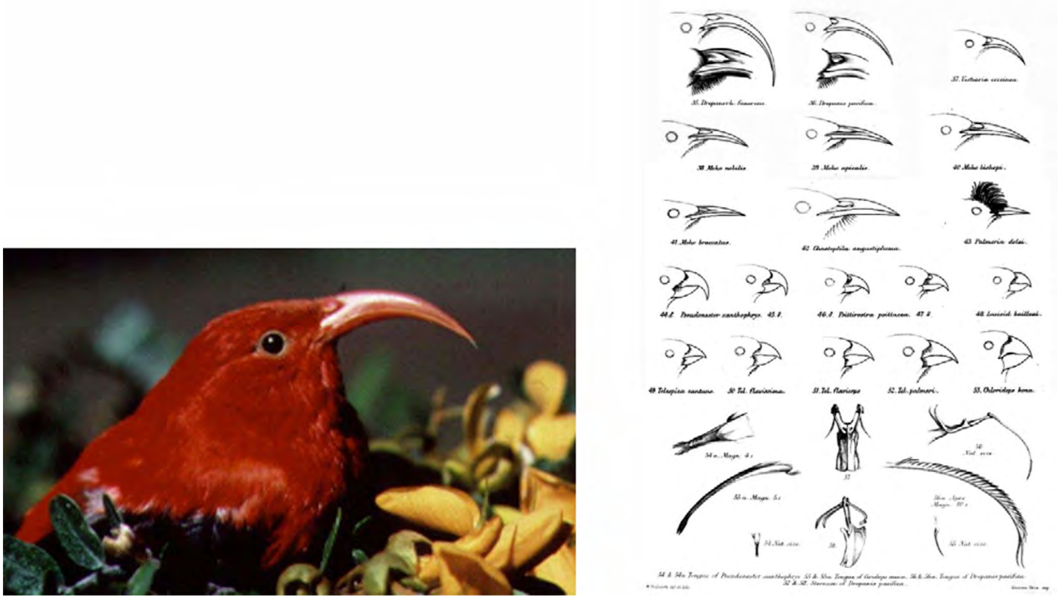

Figure 6.2: The scarlet Hawaiian honeycreeper *Drepanis coccinea* (left), and beak and tongue variation in Hawaiian honeycreepers (right). (Wikipedia 'Hawaiian honeycreeper;' Attributions: U.S. Geological Survey and John Gerrard Keulemans, respectively)

On islands, small organisms tend to exhibit gigantism and large organisms tend to exhibit dwarfism, a trend known as the "island rule" or Foster's rule, after J.B. Foster. In a 1964 paper, Foster suggested that this pattern can be explained by decreased predation pressure (due to absence of predators that are present on the mainland), which allows small animals to evolve larger body sizes, and reduced food resources, which provides selective pressure for smaller body size in large animals. But more recent research suggests that this is an oversimplified explanation of more complex causation.

There are many examples, both extant and extinct, of the island rule, from a variety of taxa. These include giant (30+ cm and 1 kg) shrew relatives in the genus *Solenodon* (Fig. 6.3, left) on the Caribbean islands, and the elephant birds and moas of Madagascar and New Zealand, respectively. The extinct dodos of the island of Mauritius were close relatives of pigeons. Gigantism in the insect world includes the giant wetas of New Zealand, relatives of grasshoppers and katydids. Island plants often exhibit gigantism and "insular woodiness;" mainland relatives are herbaceous, but the island species are woody. The cactus tree of the Galápagos and some silverswords of the Hawaiian Islands are examples. On the other hand, the extinct Channel Island, or pygmy, mammoth (Fig. 6.3, right) was only about as tall at the shoulders as an adult human, with less than one-sixth the weight of its full-sized ancestor on mainland North America. The Bali tiger, an extinct tiger subspecies, weighed no more than 100 kg, less than half the size of mainland tiger subspecies. There are several examples of dwarf island dinosaur fossils as well. Finally, evidence of island dwarfism in humans is found in *Homo floresiensis*, an extinct species of hominin descended from *Homo erectus* on the island of Flores in Indonesia.

Figure 6.3: Examples of insular gigantism and dwarfism: The shrew-like *Solenodon paradoxus* (left) and a skeleton of the Channel Island or pygmy mammoth, *Mammuthus exilis* (right). (Wikipedia 'Hispaniolan solenodon' and 'Pygmy mammoth;' Attributions: Seb az86556 and Franko Fonseca, respectively)

6.4 PATTERNS OF SPECIES RICHNESS ON ISLANDS

A major focus of island biogeography has been to unravel the factors that determine species richness on islands. There is a well-known relationship between island area and species richness; in general, larger islands have greater species richness than do smaller islands. But island area alone does not give a complete picture of insular species richness. Compared to less remote islands, very isolated islands have lower diversity than one would predict based only on their areas. The 19th century botanist Joseph Hooker noted the latter pattern with regard to plant diversity on islands, and since then this pattern has been verified for various animal taxa as well.

In 1967, ecologists Robert MacArthur and E.O. Wilson published their influential book, *The Theory of Island Biogeography*, in which they proposed that island species richness is determined by rates of species immigration and extinction. They reasoned that, as species richness (S) on an island increases, immigration of new species (I) decreases because it becomes more likely that any newly-arriving individuals belong to a species that is already present on the island. The extinction rate (E), on the other hand, will increase with S because more species means smaller population sizes for each species, increasing the risk of extinction. Immigration and extinction result in continual turnover in the species composition of an island, but the balance of these two factors results in a dynamic equilibrium level of species richness, S^* (Fig. 6.4).

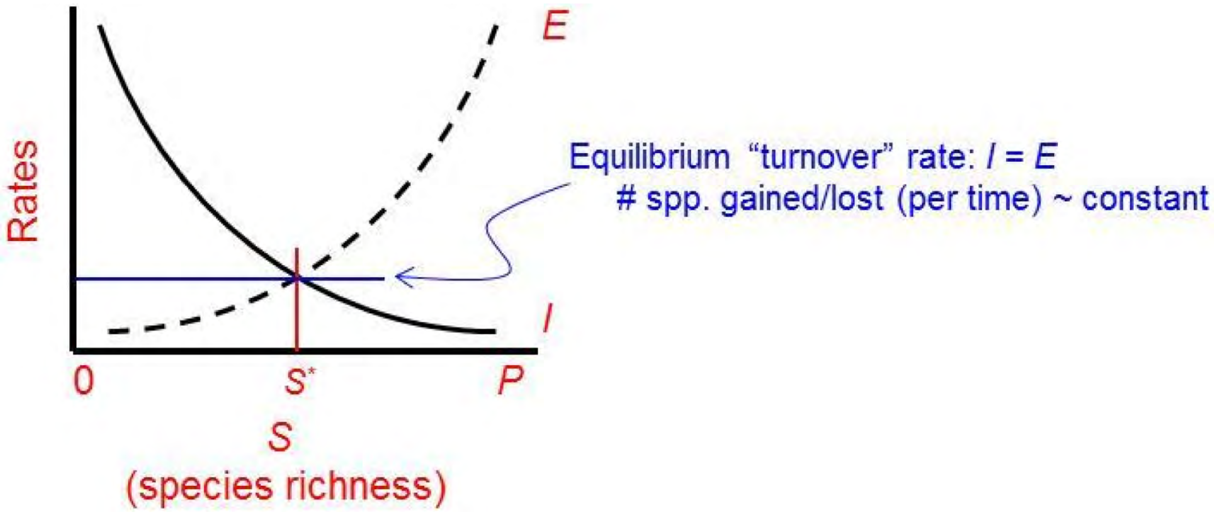

Figure 6.4: According to MacArthur and Wilson's equilibrium theory of island biogeography, species richness (S*) on an island is a result of immigration rate (*I*) equaling extinction rate (*E*). (Attribution: Shawn Meagher, Western Illinois University)

MacArthur and Wilson then included the effects of island isolation and size on immigration and extinction rates. They reasoned that immigration is affected primarily by distance of an island from a mainland source of immigrants, and extinction is determined primarily by island area. Islands that are close to a source of colonizers are more likely to receive immigrants because these islands represent a "closer target;" larger islands are less likely to have extinctions because they have more resources and environmental stability than do smaller islands. This means that greater species richness will be found on larger islands near the mainland and less richness on smaller islands far from the mainland (Fig. 6.5). Thus, MacArthur and Wilson's theory tied together island area and degree of isolation into a predictive model of island species richness.

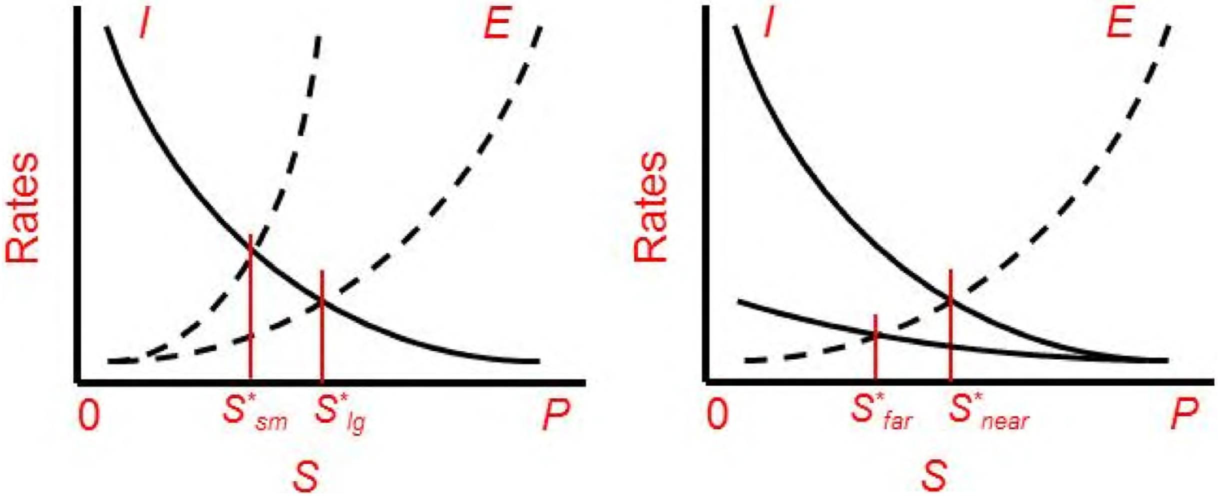

Figure 6.5: As shown by the figure on the left, larger islands will have lower extinction rates (*E*), and therefore greater equilibrium species richness (*S**), than will smaller islands. In the figure on the right, we see that islands near a mainland source of colonizers will have greater immigration rates (*I*) and greater equilibrium species richness than will more isolated islands. (Attribution: Shawn Meagher, Western Illinois University)

The theory of island biogeography has had a huge impact on biogeography and ecology, as witnessed by the new research it has generated and the many thousands of citations the book has received. The theory has been criticized for treating individual species as identical units, without taking into account differences in life histories, resource requirements, physiological constraints, and so forth. But like any scientific theory, the theory of island biogeography attempts to reveal general principles at the expense of such complex details that might mask patterns. Tests of the theory have been inconclusive, with some studies supporting the theory and others not. In general, the relationships between island size and isolation and species richness have been supported for a variety of taxa. Some studies of bird richness on islands have suggested that substantial species turnover and dynamic equilibrium does occur over time, but these studies may have been affected by anthropogenic changes on the islands. Some have expressed doubt that an island ever reaches equilibrium species richness because of the frequency of disturbances.

Of major importance is the fact that applications of the theory of island biogeography are not restricted to oceanic islands alone, but have great ramifications for insular terrestrial habitats as well. We will discuss this more fully in chapter 8.

6.5 THE MARINE ENVIRONMENT

The field of marine biogeography has progressed much more slowly than has its terrestrial counterpart. This is understandable; for humans, the marine environment is much less hospitable and accessible than most terrestrial environments. We are not adapted to breathing in water, and so must have specialized equipment in order to remain under water for very long. The tremendous physical pressure in the deep oceans has made those environments inaccessible until the relatively recent development of underwater vessels capable of withstanding such pressures. The last few decades have seen rapid and exciting developments in the field of marine biogeography.

There are several differences between marine and terrestrial environments that must be taken into account to fully understand the biogeography of marine organisms, apart from the obvious one that water is wet and air is dry ☺. One significant difference is the great importance of the vertical dimension in the oceans. On land, there is a vertical dimension associated with plant structure, flying animals, and other airborne organisms. But on land, “what goes up must come down,” and the horizontal dimension associated with the land surface, plant cover, and so forth, dominates. In the marine environment, the buoyancy provided by water makes it about as easy for many organisms to move and maintain their positions vertically as horizontally. Furthermore, as we shall see, the physical properties of water create fairly distinct vertical stratification that affects the distributions of marine organisms. Another important characteristic of the oceans is that there are fewer physical barriers to dispersal; compared to land, the marine environment is more continuous.

In general, marine organisms are much less familiar to us than are terrestrial organisms, mostly because the marine environment is less accessible to us than the terrestrial environment. The physical properties of the marine environment also provide selective pressures for traits that often seem bizarre from our perspective. Gas exchange structures are a case in point. Because aquatic organisms are surrounded by water, desiccation is of little concern. The body wall is generally very thin, and gas exchange often occurs directly across this surface. Even specialized gas exchange structures of marine animals are simply vascularized, thin-walled extensions of the body wall. These structures are usually external and in direct contact with the surrounding fluid. But terrestrial animals have a problem – the ever-present danger of desiccation in the relatively dry surrounding air. Therefore, selective pressures have favored the evolution of internal respiratory structures that are protected from the surrounding dry air. Likewise, reproduction in marine environments generally involves external fertilization, with gametes released directly into the water. In terrestrial environments, desiccation of gametes is a danger in open air, so internal fertilization is the norm. Also, marine animals generally eliminate metabolic wastes as ammonia. Ammonia is toxic; even low concentrations in the body are toxic to most animals. But marine animals can constantly eliminate ammonia because water for dilution is plentiful. Many marine animals can excrete ammonia right across the body surface. However, because desiccation is such a concern in the terrestrial environment, land animals cannot afford to expend large amounts of water diluting ammonia. Terrestrial animals generally eliminate ammonia as uric acid or urea, which require less water. They also require more complex excretory systems than do marine animals.

Other differences between marine and terrestrial animals relate to the greater density of water compared to air. This means that marine animals require less rigid skeletons, because water provides much of the support against the force of gravity. The density of water also makes possible the free-floating existence of planktonic marine organisms, as well as the suspension-feeding stationary, or sessile, animals, such as sponges and sea anemones, that feed on these abundant planktonic organisms. On land, air just doesn't contain enough of these planktonic organisms to support such suspension-feeding strategies, although orb-weaving spiders could be considered a notable exception.

6.6 STRUCTURE OF THE MARINE ENVIRONMENT

As mentioned previously, the vertical component of the marine environment is a critical factor in the distribution of marine organisms, as is proximity to the landmasses. Two basic biogeographical realms of the oceans can be recognized – the **neritic realm**, which consists of shallow seas associated with continental shelves, and the **pelagic**, or open ocean, realm. The ocean floor has much different ecological communities than those existing up in the water column. Organisms associated with the ocean floor are referred to as **benthic**, whereas those that live up in the water column are known as **pelagic**. Pelagic organisms can be **nektonic** (active swimmers) or **planktonic** (drifting organisms). In general, planktonic organisms are tiny or even microscopic, whereas nektonic organisms mostly include vertebrates and large invertebrates.

The ocean floor varies tremendously in depth. The continental shelf region, which is basically a submerged extension of the continents, slopes down to about 200 m in depth. At the shelf break, the rate of descent increases dramatically along the continental slope until reaching the abyssal plain, which ranges from about 4,000 to 6,000 m depth. But there are regions of the ocean floor that are even deeper. The deep ocean trenches are subduction zones where old ocean floor disappears into the Earth. These trenches can be over 10,000 m in depth (Fig. 6.6). The deepest of these, the Mariana Trench of the western Pacific Ocean, reaches depths of about 11,000 m.

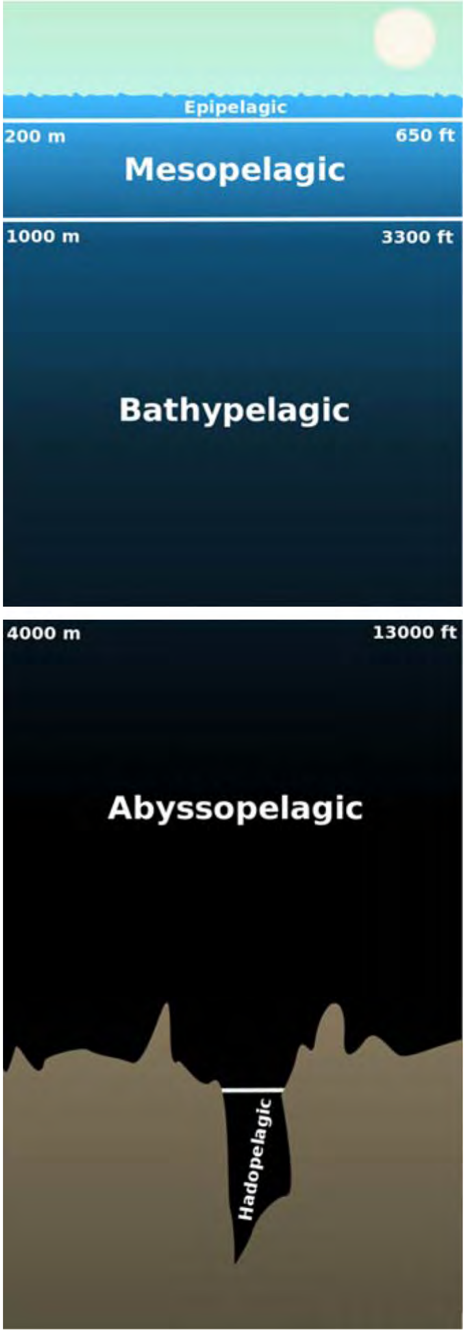

Figure 6.6: Layers of the pelagic realm. (Wikipedia ‘Pelagic zone;’ Attribution: DieBuche, Finlay McWalter, & TomCatX)

Environmental conditions vary depending on depth and proximity to landmasses, and abundance and diversity of benthic and pelagic organisms vary with these conditions as well. Light penetrates the ocean waters to only a limited extent. In the neritic realm, the waters are well-lit, and high photosynthetic rates occur here. Oxygen is generally abundant, and, except for the intertidal zone, conditions are relatively stable. The photosynthetic organisms, as well as nutrients originating from the continents, provide abundant sources of nutrients and energy for the marine life there. Compared to the pelagic realm, the neritic realm has greater abundance and diversity of life per unit volume. The irregular shapes of the continents can form isolated communities along the coastlines, and neritic communities of different landmasses are also isolated from each other, resulting in greater chances of genetic isolation and speciation among neritic communities than in the pelagic realm. For example, the neritic faunas of islands often exhibit a high degree of endemism, as does the Red Sea, a semi-isolated inlet of the Indian Ocean which is connected to the Ocean via the narrow Bab el Mandeb strait and the Gulf of Aden. Because of the high evaporation rate and little input of fresh water, the Red Sea is highly saline, providing a unique environment for it biota. The Red Sea fauna exhibits a high degree of endemism – about 17% of Red Sea fish species and 50% of cephalopod species are found nowhere else.

Within the pelagic realm (Fig. 6.6), the ocean layer in which enough light is available for photosynthesis is known as the **epipelagic zone**. Because this is the zone in which photosynthesis can take place, it contains the highest concentration of marine life in the pelagic realm. Photosynthetic phytoplankton are abundant in this zone, as well as the zooplankton that feed on them. These tiny organisms serve as the base of food chains that include larger invertebrates such as jellyfish as well as a diversity of fish species. The depth of this zone varies, but generally reaches around 200 m. Below this is a zone of twilight conditions, where little light penetrates – the **mesopelagic zone** (Fig. 6.6). Within the mesopelagic zone, there is insufficient light for photosynthesis to occur. This zone extends down to roughly 1,000 m depth, and is associated with a region of rapid water density change called the **pycnocline**. Within the pycnocline, water temperatures decrease dramatically with depth. Since cold water is denser than warm water, this rapid decrease in water temperature results in a change in water density from lower density warm waters to higher density cold waters. The pycnocline acts as a barrier, inhibiting vertical water circulation and affecting the vertical movement and distribution of chemicals and marine animals. Animals that frequent the mesopelagic zone include detritivores that feed on dead organisms and wastes descending from the epipelagic zone, and predators that in turn feed on these detritivores. These mesopelagic animals include various species of squid and cuttlefish, as well as fishes such as lancetfish, daggertooths, and lanternfish. Mesopelagic fish often have large eyes and binocular vision, particularly visual predators that must detect prey in the low light conditions. Many mesopelagic fish undertake vertical migrations, moving up to the epipelagic zone at night to feed on zooplankton and then back to the mesopelagic zone, where there is more safety from predators, during the day.

Below the mesopelagic zone lies a realm of almost total darkness. The **bathypelagic zone** (Fig. 6.6) extends down to about 6,000 m. No photosynthesis takes place here, and, per unit volume, there is much less abundance and diversity of organisms than is found in the epipelagic zone. Bathypelagic food chains are supported by the relatively small amounts of detritus, or “marine snow,” that make it down to this zone. Waters are cold; temperatures average about 4°C, with little variation. The characteristics of species inhabiting this zone reflect the selective pressures applied by these conditions. Metabolic rates and activity levels of animals in the bathypelagic zone are generally low, an adaptation for energy efficiency in an environment where food is not very abundant, and temperatures and dissolved oxygen levels are low. The skeleton (if present) and muscle tissues of bathypelagic animals are generally weak with high water content, which allows these animals to survive in the crushing water pressures at these depths. Fishes that inhabit the mesopelagic zone depend primarily on detection of sound and water pressure changes to sense their environment, and chemical detection can be important in locating mates or prey. Most animals in this zone have poorly developed vision, or no eyes at all. However, some can detect light, and some predators take advantage of this by employing bioluminescence to attract prey. Some anglerfish (Order Lophiiformes) have a bioluminescent lure that serves this function (Fig. 6.7). When the prey approaches close to the lure, the anglerfish eats it whole with its huge, tooth-filled jaws. Despite their ferocious appearance, most anglerfish are only a few centimeters long, with the male usually much smaller than the female. In some species, such as the humpback anglerfish, *Melanocetus johnsonii* (Fig. 6.7), mating occurs via the tiny male (barely 3 cm long) attaching to the body wall of the much larger female (about 18 cm long). The male becomes a symbiont of the female, deriving nutrition from her and basically becoming a sperm provider. In general, there are relatively few fishes inhabiting the bathypelagic zone. This zone is dominated by various species of whales and invertebrates such as cephalopods, brachiopods, sponges, and echinoderms.

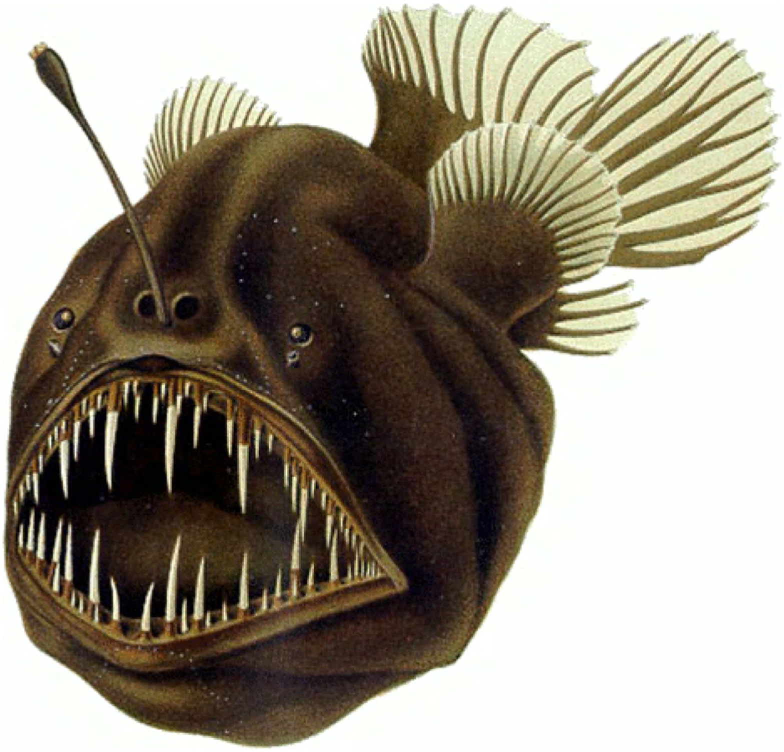

Figure 6.7: Humpback anglerfish, *Melanocetus johnsonii*.
(Wikipedia ‘Humpback anglerfish;’ Attribution: August Brauer, 1906)

Believe it or not, there are even more extreme ocean depths. The **hadopelagic zone** (Fig. 6.6) is found in the deep ocean trenches, at depths down to 11,000 m. Conditions at these depths are generally similar to those of the bathypelagic zone, only more extreme in terms of pressure and low nutrient levels, which again are dependent on the relatively little "marine snow" that filters down from above. At these depths, animal life is poorly known, and invertebrates such as annelid tube worms, jellyfish, and sea anemones dominate. A high proportion of species in the hadopelagic zone are endemics that are confined to isolated locations along the trenches.

At the other end of the "ocean floor conveyor belt" are the mid-ocean ridges. These ridges are underwater mountain systems with a valley or rift along the spine that functions as a spreading center where new seafloor is being produced. Mid-ocean ridges are volcanically active, and at some locations along the rift, fissures in the rock allow cold water to penetrate. When the water contacts the upwelling magma, water temperatures may exceed 400°C. These locations where geothermally heated water exits are known as hydrothermal vents (Fig. 6.8). Previously we pointed out that photosynthesis doesn't occur below the epipelagic zone because of lack of sunlight. But these hydrothermal vents are home to unique ecological communities that are far more diverse than could be supported by the sparse marine rain they receive. How do these communities persist without a base of photosynthesizing organisms? The dissolved minerals contained in the water support chemosynthetic bacteria. These amazing bacteria are the primary producers of the vent community. Rather than using light to produce energy, these organisms use chemicals, such as hydrogen sulfide produced by the hydrothermal vents, to produce energy, and are fed upon by invertebrates such as copepods and amphipods. In turn, these tiny invertebrates support food chains of larger animals, resulting in vibrant ocean floor communities that include tubeworms, snails, crabs, a variety of other invertebrates, and various fish species.

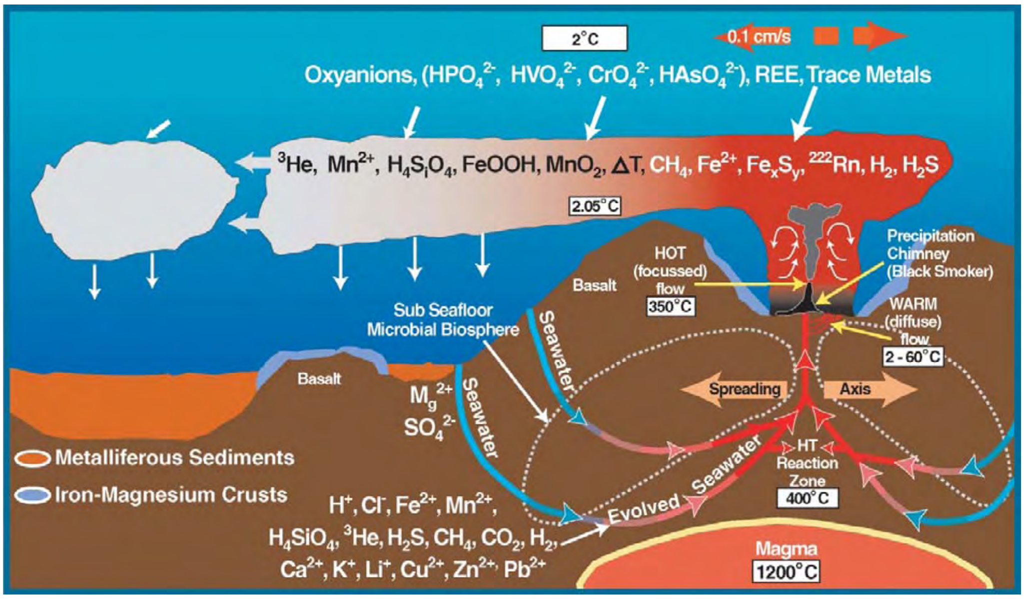

Figure 6.8: Diagram of hydrothermal vent biogeochemical cycle. (Wikipedia 'Hydrothermal vent;' Attribution: U.S. National Oceanic and Atmospheric Administration)

The biological diversity of hydrothermal vent communities is impressive, but pales in comparison to that of the "rainforests of the oceans," the coral reefs (Fig. 6.9). As the name would suggest, coral reefs are formed by reef-building stony corals, tiny, colonial members of the Phylum Cnidaria, which also includes jellyfish and sea anemones. These corals secrete a calcium carbonate skeleton that forms a hard outer shell covering the colony. It is this skeleton, along with other organisms such as coralline algae and shelled molluscs, that provides the reef structure. Coral reefs are widespread, but are most abundant in shallow, clear tropical waters. The greatest concentration of coral reefs is in the Australian/Indonesian region, with the Indian Ocean and the Caribbean Sea also containing substantial reefs (Fig. 6.10). Coral reefs comprise less than 0.1% of the total ocean surface, but contain over 25% of marine species.

Figure 6.9: A blue starfish (*Linckia laevigata*) resting on hard acropora coral. Lighthouse, Ribbon Reefs, Great Barrier Reef. (Wikipedia 'Great Barrier Reef;' Attribution: Copyright (c) 2004 Richard Ling; www.rling.com)

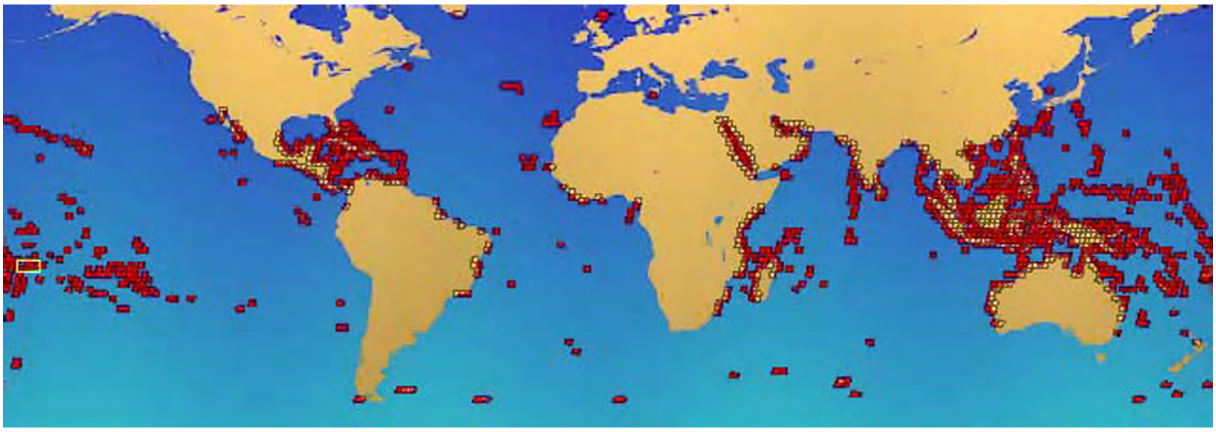

Figure 6.10: Locations of coral reefs. (Wikipedia 'Coral reef;' Attribution: U.S. National Aeronautics and Space Administration)

Paradoxically, coral reefs thrive in nutrient-poor waters. Corals can absorb some nutrients directly from the water, and they also catch zooplankton with their tentacles. But endosymbiotic dinoflagellates, mostly in the genus *Symbiodinium*, are a major source of energy for the corals. These single-celled, photosynthetic protists reside in the tissues of tropical corals, and provide a significant amount of energy to the corals. The corals, in return, provide their endosymbiotic mutualists with nutrients, CO_2, and an advantageous location for receiving sunshine. These endosymbionts are sensitive to environmental conditions, and changes in water chemistry, temperature, salinity, and other factors can trigger the loss of these zooxanthellae, a process known as "coral bleaching." The corals can sometimes be recolonized by zooxanthellae if conditions improve, but long-term or repeated bleaching can result in death of the corals. Because coral reefs provide so much of our marine biodiversity, coral bleaching is a serious problem associated with pollution, other anthropogenic changes in water quality, and climate change.

In the last couple of chapters, we have focused primarily on biogeographic patterns from an ecological perspective. In the next chapter, we will consider longer term historical factors that have played important roles in shaping the distribution of Earth's biodiversity.

6.7 REFERENCES AND FURTHER READING

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7 HISTORICAL BIOGEOGRAPHY

Your goals for this chapter are to learn about:

- Early life on Earth
- The Cambrian Explosion
- Major tectonic, climatic, and biogeographical patterns of the Paleozoic Era
- Major tectonic, climatic, and biogeographical patterns of the Mesozoic Era
- Major tectonic, climatic, and biogeographical patterns of the Cenozoic Era
- The Great American Interchange
- Milanković cycles

7.1 INTRODUCTION

The patterns of biodiversity that we see today are, to a great extent, the result of historical events that have occurred over hundreds of millions and even billions of years. In this chapter we will take a broad overview of the four billion year history of life on Earth, and connect these historical events with present-day biogeographical patterns.

7.2 EARLY LIFE AND BIOGEOGRAPHY OF THE PALEOZOIC ERA

Precambrian Supereon

The planet Earth formed about 4.6 billion years ago (BYA), but life didn't appear for approximately another 600 million years, late in the Hadean Eon. Early single-celled organisms were chemosynthetic, oxidizing inorganic materials for energy. The last universal common ancestor appeared in the early Archean Eon. Fig. 7.1 shows a phylogenetic tree linking major taxa to the last universal common ancestor, based on completely sequenced genomes. By 3.5 BYA, prokaryotes, bacteria and archaea had appeared, and some bacteria were photosynthetic, although they did not produce oxygen as a byproduct. Photosynthetic oxygen-producing cyanobacteria appeared about 3 BYA, eventually paving the way for aerobic organisms. Single-celled eukaryotes first came on the scene in the Proterozoic Eon, about 2 BYA. Complex multicellular organisms had appeared by the late Proterozoic.

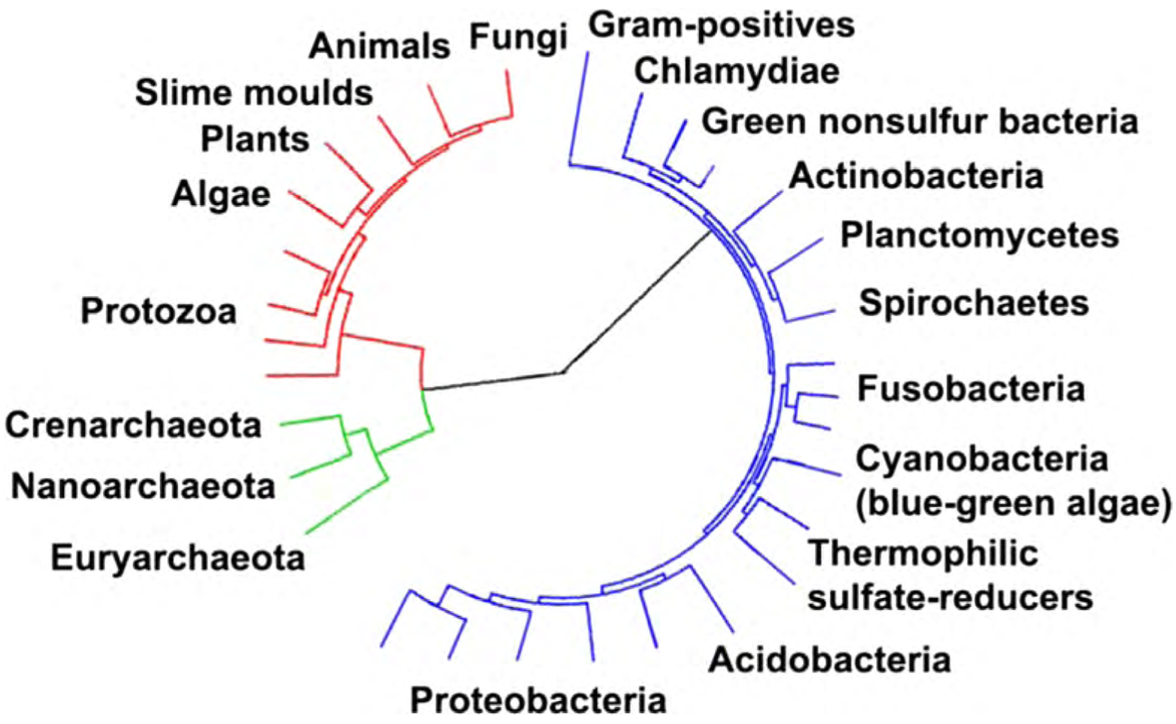

Figure 7.1: Phylogenic tree of life. Eukaryotes are colored red, archaea green and bacteria blue. The central node represents the last universal common ancestor.
(Wikipedia 'Phylogenetic tree;' Attribution: User A1)

Cambrian period

The Phanerozoic Eon opened with the Cambrian Period of the Paleozoic Era, ca. 540 million years ago (MYA). See Fig. 5.12 for timeline of geological periods. The Cambrian Period opened with the Cambrian explosion, a relatively brief (20 to 25 million year) evolutionary event in which major diversification occurred in the oceans, leading to the appearance of most modern animal phyla. Included among these were the vertebrates (Phylum Chordata) and the Phylum Arthropoda, such as *Opabinia* (Fig. 7.2), a close relative of the ancestral arthropods. Climatically, the early Cambrian was cold, but would warm near the end of the period. Most land mass was concentrated in the Southern Hemisphere early on, but over time separation occurred with the land masses gradually moving north. Plants had yet to invade land in the Cambrian, but fungi and microbes were beginning to contribute to soil formation that would pave the way for terrestrial plants. The dominant animal life in the oceans consisted of arthropods such as trilobites (Fig. 7.3), although the trilobites are probably overrepresented in the fossil record because of their heavy exoskeletons. Chordates and various shelled animals appeared in the oceans during the Cambrian, and the first vertebrates arrived on the scene in the form of the jawless, armored ostracoderms. Several extinction events caused a dramatic decline in marine diversity in the late Cambrian.

Figure 7.2: Artist's impression of *Opabinia*, a close relative of the ancestral arthropods, at the sea floor. (Wikipedia '*Opabinia*;' Attribution: Nobu Tamura)

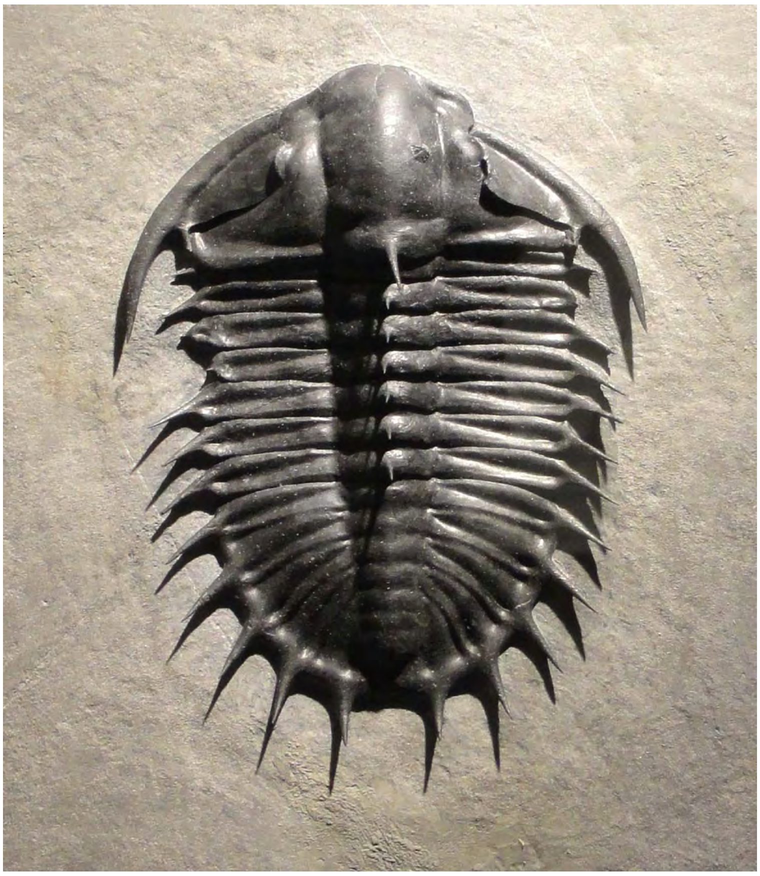

Figure 7.3: *Olenoides superbus*, a trilobite from the Cambrian period. (Wikipedia '*Olenoides;*' Attribution: Daderot)

Ordovician period

The Ordovician Period began ca. 485 MYA. By this time, southern continents were clustered into a single landmass, Gondwana, which began the period near the equator, but gradually drifted southward. The more northern landmasses, Laurentia (which would eventually become present day North America), Siberia, and Baltica (eventually to be northern Europe) were still separated. High levels of CO_2 and the accompanying greenhouse effect produced generally high temperatures during the early Ordovician, with ocean temperatures probably well over 40°C. But by the mid-Ordovician the climate had cooled considerably, and the ensuing glacial advances probably contributed to the large-scale extinction events during the latter part of the period.

Green algae were abundant in the Ordovician, and gave rise to the early non-vascular plants that colonized shoreline areas in the late Ordovician-early Silurian. Early mycorrhizal fungi helped facilitate this invasion through symbiotic relationships with plant roots, helping the plants obtain nutrients. In the animal world, significant adaptive radiation took place in the oceans during the period, with various filter feeding groups such as crinoids, brachiopods, and bryozoans becoming abundant, as well as early cephalopods and corals. Shelled molluscs such as bivalves, gastropods, and nautiloid cephalopods diversified as well. Trilobites remained abundant, especially in the shallow continental seas, with many forms evolving elaborate defenses, such as spines and stalked eyes, in response to the growing number of predators. The first jawed fish appeared in the late Ordovician.

The end of the Ordovician is marked by the Ordovician extinction, the second largest mass extinction in the Earth's history. Probable causes of these extinction pulses were glaciation associated with cooling temperatures. These cooling temperatures were likely the result of multiple factors. These include an increase in volcanic activity and an associated decrease in CO_2 (a greenhouse gas) in the atmosphere, and the position of Gondwana over the South Pole, which resulted in ice caps that increased the Earth's albedo. The high volcanic activity deposited large amounts of silica rock, which draws CO_2 from the atmosphere during the erosion process. This decrease in CO_2 in turn reduced the greenhouse effect. One effect of glaciation was a decrease in ocean levels, which in turned caused a decline in the shallow continental seas that supported so much of Ordovician biodiversity.

Silurian period

The Silurian Period began ca. 444 MYA. During this period, Gondwana remained intact, covering much of the equatorial and southern hemisphere regions. Further north, a second supercontinent, Euramerica (also known as Laurussia, not to be confused with the later supercontinent Laurasia), was forming through the collision of several tectonic plates. The climate during much of the Silurian was generally warm and stable, and melting ice caps increased ocean levels. Later in the period, cooling resulted in lowering of ocean levels.

Late in the Silurian, vascular plants (land plants that have specialized vascular tissues that conduct water and nutrients) appeared and diversified. The first recognizable fossils of land animals were arthropods that also appeared in the late Silurian. The arthropod exoskeleton provided effective pre-adaptations for support, resistance to desiccation, and efficient locomotion on land. These are important features for organisms surrounded by dry air and at the mercy of gravity without the buoyancy that water provides. Sea scorpions (eurypterids) were abundant predators in the oceans, particularly shallow sea habitats. Some of these arthropods reached over 2 m in length. Also in the oceans, suspension feeders such as brachiopods, bryozoans, and crinoids remained abundant and diverse, as well as trilobites and molluscs. The first bony fish appeared in the form of the Acanthodii, shark-like fish with skeletons that had cartilaginous as well as bony components.

Devonian period

The Devonian Period began roughly 420 MYA, at a time when Euramerica and Gondwana were moving together (Fig. 7.4) to eventually form the giant supercontinent Pangaea. This period was relatively warm and glacier-free, with high ocean levels. In the marine environment, jawed fish and armored placoderms were abundant, although the placoderms would disappear by the end of the period. The Devonian is often referred to as the "age of fishes" because of the great diversity of this group during the period. Among the marine invertebrates, brachiopods, bryozoans, crinoids, trilobites, and corals continued to be abundant, and ammonites (primarily spiral-shelled cephalopods) first appeared.

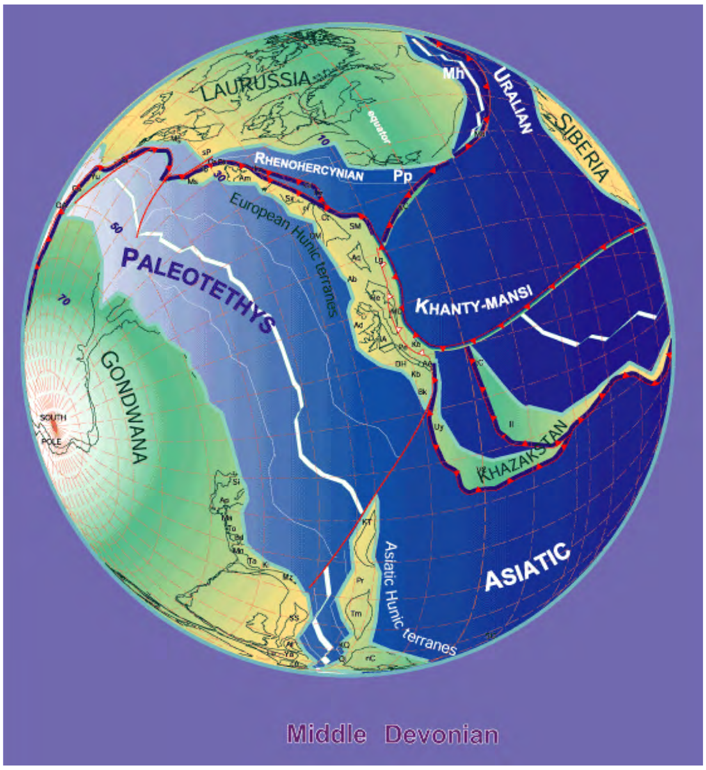

Figure 7.4: Positions of the landmasses and Paleotethys Ocean during the middle Devonian (Wikipedia 'Devonian;' Attribution: http://www-sst.unil.ch/research/plate_tecto/alp_tet_main.htm#Introduction)

In the terrestrial environment, plant colonization and diversification accelerated. Rooted plants were contributing to further soil development. By the mid-Devonian, shrubby forests consisting of ferns, horsetails, lycophytes, and progymnosperms had appeared. In the late Devonian, the first true trees would appear in the form of certain progymnosperms that would eventually give rise to the true gymnosperms. By the end of the period, the first seed plants (land plants that produce embryos with a protective outer covering) had appeared. The well-developed soils harbored mites, myriapods, and other arthropods. The first probable insects appeared in the early Devonian; this would lead to the long coevolutionary relationship between insects and plants. The first tetrapods, evolving from lobe-finned fish in shallow coastal waters, had appeared by the mid-Devonian as well.

Carboniferous period

The Carboniferous Period began ca. 359 MYA. The period is named for the abundance of coal deposits that formed as a result of burial of lowland forests under soil. This eventually resulted in trapped carbon in buried peat bogs. High pressures and high temperatures converted this dead vegetation to coal. During the Carboniferous, the single supercontinent Pangaea was forming. The early Carboniferous was relatively warm, with high ocean levels, but a cooling trend occurred in the mid-Carboniferous. Lowering ocean levels led to a large marine extinction. The cooler, drier climate also led to the Carboniferous rainforest collapse, in which the extensive rainforests of the Euramerican equatorial belt were fragmented into smaller and smaller islands. Lycophytes disappeared and tree ferns (not to be confused with *Glossopteris* and other seed ferns) became dominant. Among the tropical animals, amphibians declined while reptiles increased in abundance and diversity. Plant life of the early Carboniferous was dominated by horsetails, club mosses, and ferns, with cycads, conifers, and the tree-like lycopodiophyte *Sigillaria* (Fig. 7.5) appearing later in the period. The Division Lycopodiophyta is the oldest extant vascular plant division.

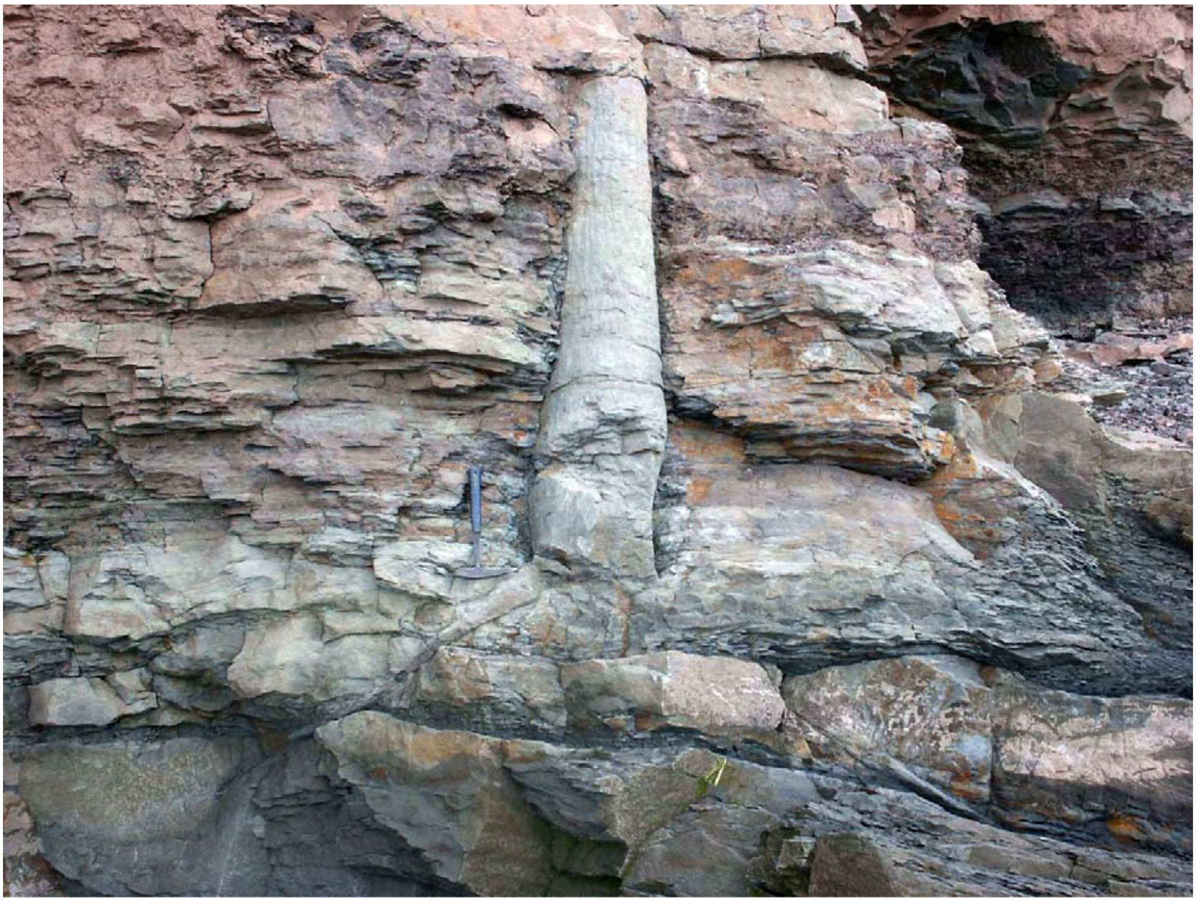

Figure 7.5: Ancient *in situ* Lycopodiophyta, probably *Sigillaria*, from the Joggins Formation (Pennsylvanian), Cumberland Basin, Nova Scotia. (Wikipedia 'Carboniferous;' Attribution: Michael C. Rygel via Wikimedia Commons)

Most of the dominant Devonian marine invertebrates, such as brachiopods, bryozoans, and crinoids, continued to be abundant in the Carboniferous, and bivalve molluscs increased in importance. However, by this time the trilobites were declining toward their eventual extinction at the end of the Permian. Bivalve molluscs were becoming abundant in freshwater environments as well, and amphibious sea scorpions (eurypterids) were also common in these habitats. Shark diversity increased dramatically in the Carboniferous oceans, possibly as a result of open ecological niches left by the extinction of the placoderms.

On land, insects and other arthropods were abundant, and some of these reached unusually large sizes. These included millipede-like arthropods over 2 m in length, and some of the dragonfly-like griffinflies, which had wingspans of well over a half meter. Explanations for these unusually large insects are still under debate. One possibility is the very high oxygen content of the atmosphere at this time. Insects obtain oxygen primarily by diffusion through their tracheal system, a network of tubes that runs throughout the body. The rate of oxygen diffusion places an upper limit on insect body size, a limit that would have been relaxed in the high oxygen environment of the Carboniferous. It has also been suggested that the absence of flying vertebrate predators played a role in allowing these flying insects to evolve such large body sizes.

Among the vertebrates, amphibians were abundant and diverse in the early Carboniferous, but declined as a result of the aforementioned rainforest collapse. In contrast, a major evolutionary innovation allowed reptiles to survive and flourish in drier environments. This was the amniote egg, with a sturdy outer shell and sac-like allantois that prevented desiccation while still allowing gas exchange and waste storage. The pelycosaurs, an early synapsid (tetrapods with one or more fenestrae, or holes, in the temporal bone of the skull) amniote group, appeared in the late Carboniferous. The synapsids would give rise to the therapsids, a lineage that would lead to the mammals.

Permian period

The Permian period, the last period of the Paleozoic Era, began ca. 299 MYA. During the Permian, the landmasses were formed into one supercontinent, Pangaea (Fig. 7.6). The existence of a single landmass contributed to a continental climate with extremes of heat and cold, and increased aridity in the interior regions. These conditions in turn played a great role in the evolutionary patterns shown by many plant and animal groups. At the beginning of the period, the cool temperatures and extensive glaciation from the end of the Carboniferous continued; later in the Permian, dry conditions and cycles of warm and cold temperatures predominated.

Figure 7.6: Early formation of Pangaea, about 290 million years ago in the early Permian. (Wikipedia 'Paleo-Tethys Ocean;' Attribution: http://www-sst.unil.ch/research/plate_tecto/alp_tet.htm)

In the marine environment, many of the groups that were dominant in the Carboniferous continued to be predominant. Corals, echinoderms, and molluscs were abundant; these animals, as well as brachiopods, sponges, foraminiferans, and bryozoans formed rich shallow-water reef communities. Bony fishes continued to diversify. On land, the dry continental conditions favored the diversification of seed plants such as conifers, seed ferns, and cycads. Insects were abundant, particularly various cockroach-like groups. Early in the period, amphibians were abundant, but increased aridity favored reptiles. The synapsids gave rise to the therapsids; these animals had more complex skull, jaw, and tooth structure than the earlier pelycosaurs. The therapsid lineage would eventually give rise to the mammals. The Permian period ended with the Permian-Triassic mass extinction, the largest mass extinction in the Earth's history. This mass extinction probably had multiple distinct pulses or phases, causes by different factors, including global warming caused by methane (a greenhouse gas) released from permafrost and ocean sediments, volcanism, and one or more meteor impact events. This event saw the extinction of over 90% of marine species and 70% of terrestrial species; it would take many millions of years for the Earth to recover these losses in biodiversity.

7.3 BIOGEOGRAPHY OF THE MESOZOIC ERA

Triassic period

The Triassic period marks the beginning of the Mesozoic Era, and began about 252 MYA. During the Triassic, Pangaea persisted, surrounded by the world-wide ocean Panthalassa and partially bisected by the Tethys Sea (Fig. 7.7). The climate was mostly hot and dry, although there was more moisture near the poles, and periods of increased rainfall near the equator. There was little or no glaciation during the Triassic. Plant life during the period was dominated by conifers and other seed plants; the seed fern *Glossopteris* (Fig. 2.10) was abundant in the southern hemisphere. The large mass extinction at the end of the Permian opened many new ecological niches that led to adaptive radiations. In the oceans, more modern corals appeared, and ammonites remained abundant, descended from ancestors that survived the mass extinction. Reptiles diversified in the oceans and on land, ultimately evolving into the diverse forms that are the reason the Mesozoic is often referred to as the "age of reptiles." Plesiosaurs and ichthyosaurs became abundant and diverse in the marine world.

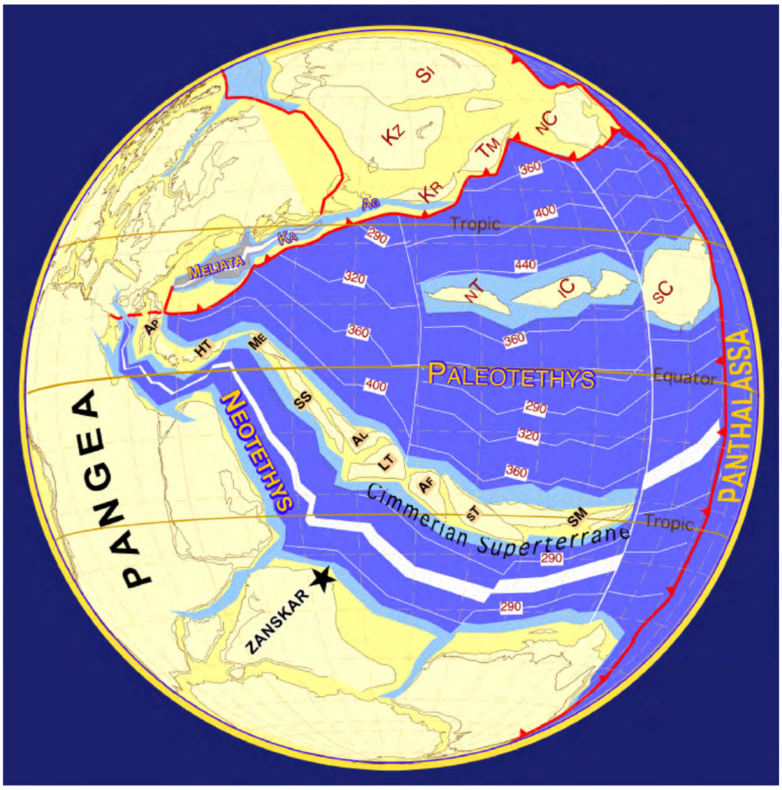

Figure 7.7: Pangaea and oceans about 249 million years ago at the Permian-Triassic boundary. (Wikipedia 'Paleo-Tethys Ocean;' Attribution: http://www-sst.unil.ch/research/plate_tecto/alp_tet.htm)

In the terrestrial environment, early semiaquatic archosaurs would diversify from their humble beginnings to eventually give rise to such dominant groups as dinosaurs and the first flying vertebrates, the pterosaurs. Archosaurs became dominant in the Triassic; their ability to eliminate nitrogenous wastes in the form of uric acid, which contains little water, was advantageous in the arid Triassic climate. Theropod dinosaurs appeared in the Triassic; this group would eventually give rise to the birds. Cynodonts, a group of therapsids that first appeared in the Permian, would increase in importance in the Triassic and eventually lead to the evolution of mammals.

Jurassic period

The Jurassic Period began about 201 MYA; its beginning is marked by the Triassic-Jurassic mass extinction. During this event, over half of all species went extinct, including all archosaurs other than dinosaurs and crocodylomorphs. Many amphibian species went extinct as well. This extinction event opened many ecological niches and made way for the diversification of the dinosaurs, which would become dominant in the Jurassic. During this period, the climate changed significantly; this was caused to a great extent by the splitting of Pangaea into two supercontinents, the northern Laurasia and southern Gondwana. This created more coastline relative to continental interior, leading to a general shift from arid to wetter conditions. As was the case in the Triassic, the Jurassic climate was generally warm, with little glaciation.

In the oceans, the dominant vertebrates were fish and marine reptiles such as ichthyosaurs and plesiosaurs. Many planktonic groups appeared and diversified. High levels of precipitated calcium carbonate produced large carbonate hardgrounds on the sea floor. This led to the increased importance of encrusting and boring communities that caused bioerosion of these hardgrounds. Rudists, a group of bivalve molluscs, appeared in the Jurassic and would become major components of reef communities. On land, many groups of ferns were present. Conifers and cycads were also common, as well as ginkgos. The latter group is represented today by one relict species, *Ginkgo biloba*, a species that is found in the wild in China, but grown as an ornamental throughout the world. The flowering plants, or angiosperms, appeared in the late Jurassic, but would not achieve dominance until the Cretaceous. Reptiles, and dinosaurs in particular, were the dominant vertebrates (Fig. 7.8). Sauropods, huge plant-eating dinosaurs such as *Brachiosaurus* and *Brontosaurus*, roamed the fern thickets and forests, and were preyed on by predatory theropods such as *Torvosaurus* and *Allosaurus*. Within the theropod clade, the first birds appeared in the late Jurassic. The first mammals also appeared, primarily in the form of nocturnal insectivores.

Figure 7.8: Various dinosaurs roamed forests of similarly large conifers during the Jurassic period. (Wikipedia 'Jurassic;' Attribution: Gerhard Boeggemann)

Cretaceous period

The Cretaceous Period began about 145 MYA and spanned 79 million years, making it the longest period in the Phanerozoic Eon. This period would see the continued separation of the landmasses, with Laurasia and Gondwana breaking up into the recognizable present day continents, although in different positions than they are today. With the exception of a cooling trend that began in the late Jurassic and extended into the early Cretaceous, the Cretaceous Period was relatively warm. This warming trend is thought to have been due primarily to the greenhouse effect of carbon dioxide produced by volcanic activity.

In the oceans, modern sharks and ray-finned fishes appeared. Marine reptiles such as ichthyosaurs and plesiosaurs (Fig. 7.9) remained dominant through most of the Cretaceous, but near the end of the period ichthyosaurs would decline, to be replaced by the mososaurs. Rudist bivalves were abundant, as were straight-shelled cephalopods in the genus *Baculites*. Sea stars and other echinoderms flourished, and diatoms diversified as well. On land, some groups of conifers and ferns continued to thrive as well. Angiosperms continued to spread and diversify, becoming the dominant group of plants by the end of the period. This coincided with the continued diversification of insects; coevolutionary relationships between angiosperms and pollinating beetles, flies, butterflies and moths, and especially bees have provided important selective pressures driving diversification. Among the vertebrates, mammals continued to radiate. But reptiles, in particular the dinosaurs, continued to remain dominant. These included such well-known dinosaurs as *Tyrannosaurus rex*, *Triceratops*, and *Velociraptor* of Jurassic Park movie fame. The pterosaurs declined in the latter part of the period; this was once thought to be due to competition with birds, but patterns of bird diversification do not appear to correspond to pterosaur decline.

Figure 7.9: *Kronosaurus queenslandicus* preying on another plesiosaur, *Woolungasaurus*. (Wikipedia 'Cretaceous;' Attribution: Dmitry Bogdanov)

The Cretaceous was brought to a close by the Cretaceous-Paleogene mass extinction. While other factors may have played a role, the widely accepted cause of this mass extinction is an asteroid impact on the coast of Yucatán, Mexico. This hypothesis was first proposed by Nobel Prize-winning physicist **Luis Alvarez** (1911–1988) and his research team, which discovered extremely high concentrations of the element iridium (an element found in high concentrations in many asteroids) in Cretaceous-Paleogene boundary sedimentary layers worldwide. Since then, their hypothesis has been supported by the presence of tiny droplets of crystalized molten rock at the boundary layer, and, finally, the discovery of a very large crater on the Yucatán Peninsula.

Such an impact would have created a cloud of dust and aerosols in the air that would have dramatically decreased the amount of sunlight reaching the Earth. The disturbance would have taken years to dissipate. Extinction of photosynthetic plants and phytoplankton was accompanied by disappearance of the herbivores dependent on them, and consequently their predators. Most famously, the non-avian dinosaurs went extinct, although some paleontologists believe that some survived into the Paleocene Epoch. This would be an example of a "dead clade walking;" a taxon that survives a mass extinction and persists for a few million years, but never recovers and eventually goes extinct. However, the evidence for Paleocene dinosaurs is scant, and most paleontologists reject this argument. In the marine environment, ca. 75% of species went extinct; among land animals, only insects and other invertebrates, and small vertebrates, survived. Detritivores (animals that feed on non-living organic material, or detritus), and animals that depended on detritivores as food, fared relatively well compared to herbivores and their predators. This makes sense, for most of the available food would have been in the form of dead, rather than living, plants and animals. Recovery of biodiversity from this event was slow, but eventually the profusion of available ecological niches led to the large evolutionary radiations of the Paleogene Period.

7.4 BIOGEOGRAPHY OF THE CENOZOIC ERA

Paleogene period

The Paleogene Period was the first period of the Cenozoic Era, and began about 66 MYA. The period consists of the Paleocene, Eocene, and Oligocene Epochs. The Paleocene Epoch lasted until about 56 MYA. The epoch is bounded by the aforementioned Cretaceous-Paleogene mass extinction and the Paleocene–Eocene Thermal Maximum, a period of dramatic warming. During the Paleocene, the continents continued to break up and move toward their present-day positions. The mass extinction at the end of the Cretaceous left many available ecological niches, and during the early Paleocene the marine biota was rather impoverished. However, over time, marine biodiversity rebounded, and began to resemble our present day fauna. The demise of marine reptiles at the end of the Cretaceous opened the way for diversification of the sharks, and tropical conditions at the end of the Paleocene led to abundant and diverse vertebrate and invertebrate life, including diverse coral reef communities. Marine mammals, however, would not appear until the Eocene.

Soon after the Cretaceous-Paleogene extinction event, ferns became dominant on land; this may provide further evidence of an asteroid strike, since many ferns are known to colonize fire-disturbed areas quickly. But over time, the plant world began to take on a modern look. Palms appeared, and forest cover was abundant, including widespread rain forests late in the epoch. Angiosperms rebounded from the mass extinction event and achieved dominance, along with their insect pollinators. The small mammals and other vertebrates that survived the extinction event underwent large-scale adaptive radiations in the Paleocene, growing larger and invading available niches. These included many modern groups. Reptiles such as crocodylians, turtles, snakes, and lizards were abundant, and birds continued the dinosaur lineage, including large flightless birds such as the predatory phorusrhacids, or "terror birds." These imposing birds ranged up to 3 m in height, and were top predators in South America during the Cenozoic. Among the mammals, the first monotremes appeared, as well as early marsupials, and later the placentals. The latter group, which in time would come to dominate the world's mammalian fauna, was represented by early primate-like and insectivore-like mammals, among others. A separate lineage, the rodent-like multituberculates, also appeared, and would survive for 120 million years, the longest period of any mammal lineage. The "archaic" Paleocene mammals were still anatomically primitive and had small brains compared to most modern mammals.

The Eocene Epoch began about 56 MYA. This epoch was characterized by a widely varying climate, beginning with the very warm period during the Paleocene-Eocene Thermal Maximum (PETM), but then cooling gradually for the remainder of the epoch. During the Eocene, the high levels of CO_2 in the atmosphere that contributed to the PETM gradually decreased due to sequestration of CO_2 at the bottom of the Arctic Ocean, probably as a result of large-scale organic carbon burial. Landmasses continued toward their present-day positions, with Australia breaking away from Antarctica about 45 MYA and Laurasia beginning to separate as North America, Greenland, and Europe moved apart. India would collide with Asia, beginning the formation of the Himalayas. The high early Eocene temperatures supported widespread forests, but as the climate cooled later in the epoch, the lush evergreen tropical forests were largely replaced by deciduous forests.

In the oceans, fish continued to diversify, and marine mammals made their first appearance, including the cetaceans. On land, mammals continued to increase in importance (Fig. 7.10). The early ungulates appeared, including representatives of the modern hoofed ungulates, such as *Eohippus* ("dawn horse"). Strange carnivorous ungulates were present as well. These included *Mesonyx*, with toes that ended in small hooves instead of claws, and the giant *Andrewsarchus mongoliensis*, known only from a single large skull and some fragments of bone. Proportional to its head, the body of *A. mongoliensis* was about 3.5 m long, with a height of about 1.8 m at the shoulder. This means that *A. mongoliensis* may rival the South American short-faced bear, *Arctotherium*, for the title of largest terrestrial carnivorous mammal. Nimravids, close relatives of cats, appeared in the middle Eocene. These were predatory animals that are sometimes called "false saber-toothed cats" because they show convergent evolution with *Smilodon* saber-toothed cats in many respects. The first primates also appeared, either in the late Paleocene or early Eocene. These were represented by the small, rodent-like genus *Purgatorius*; quite a humble beginning for an order that would eventually give rise to humans. Early forms of most present day mammal orders appeared in the Eocene. Atmospheric oxygen levels were high during much of the Eocene, perhaps contributing to increased brain size, body size, and dominance of mammals, particularly placentals. Large brains require large amounts of oxygen, and high oxygen levels are also advantageous to pregnant females which must provide substantial amounts to the developing fetus. The end of the Eocene saw a large extinction event, although not at the same level as the larger mass extinctions. There appears to be a variety of potential causes for the Eocene-Oligocene extinction, including cooling climate, large-scale volcanic activity, and meteor impacts.

Figure 7.10: Depiction of the Eocene fauna of North America.
(Wikipedia 'Eocene;' Attribution: Jay Matternes)

The Oligocene Epoch, the final epoch of the Paleogene Period, began about 34 MYA. This epoch was characterized by a generally cool, dry climate compared to the rest of the Paleogene. South America detached from Antarctica and drifted north, and Antarctica became colder due to the now uninterrupted flow of the Antarctic Circumpolar Current, which isolated the continent from warmer waters. In general, the oceans cooled during the Oligocene, and as the continents continued to move toward present-day positions, ocean circulation patterns began to take on a modern look as well. A land bridge between North America and Europe allowed exchange between these two continents, resulting in increased similarity of the faunas of the two landmasses. Tectonic activity resulted in mountain formation in western North America and Europe. The more arid climate favored the continued expansion of temperate deciduous forests at the expense of tropical forests; more open grasslands and deserts increased as well.

The expansion of grasslands led to spread of animal groups associated with them, such as horses, camels, and rhinoceroses, as well as the pig-like merycoidodontoids. The first true felid, *Proailurus*, appeared in the Oligocene in Asia. This was a relatively small, partially arboreal cat, about the size of a bobcat or lynx. The isolation of South America led to the evolution of a rather unique and often strange fauna, including mastodon and rhinoceros-like species, terrestrial crocodilian relatives, and the aforementioned terror birds. Camels, rhinoceroses, and horses roamed central North America. In Asia, *Paraceratherium*, an extinct genus of hornless rhinoceros, roamed the shrublands and forests, browsing on leafy plant material. These animals were perhaps the largest terrestrial mammals that have ever existed, weighing in at 15 to 20 tons – roughly the size of a *Brontosaurus*.

In the oceans, modern groups of bivalve molluscs and polychaete worms appeared. Carcharhinid sharks appeared and began to diversify as well. This family includes roughly 60 extant species, including such well-known species as the tiger shark and oceanic whitetip shark. Cetaceans continued to diversify, and evolved echolocation, a major adaptive feature. The first pinnipeds appeared in the late Oligocene. At the end of the Oligocene the climate underwent a warming trend, but this was interrupted by a dramatic cooling event as the Earth moved into the Neogene Period and Miocene Epoch.

Neogene period

The Neogene Period and Miocene Epoch began about 23 MYA. Rather than being defined by discrete global events, the Miocene boundaries reflect regional transitions between the relatively warm Oligocene and the cooler Pliocene. During the Miocene, the continents continued to bear greater resemblance to today's configuration. Tectonic activity caused further mountain formation in western North America, Europe, and eastern Asia. South American continued to move north, and the Andes began to form as a result of contact with the western Pacific subduction zone. The Isthmus of Panama had yet to form though, so South America and North America remained separated. Climatically, the Miocene was still relatively warm, but overall a general cooling trend continued, accompanied by increasing aridity. By the end of the epoch, the Antarctic ice sheet had increased in size and thickness, and glaciers were forming in Greenland.

Rain forests continued to contract and grasslands expanded. Deeper, richer grassland soils acted as a carbon sink, reducing atmospheric CO_2 and contributing to the cooling climate. Late in the Miocene, C_4 grasses appeared and increased in importance. Relative to C_3 grasses, C_4 grasses are at a competitive advantage in arid conditions because they use water more efficiently during photosynthesis. Accompanying the expansion of grasslands were large numbers of diverse grazing ungulates (Fig. 7.11). Horses, deer and camels were abundant. The predatory nimravids persisted, as well as entelodonts, huge, pig-like animals that first appeared in the Eocene. These creatures are sometimes referred to as "terminator pigs," and reached sizes of over 400 kg and over 2 m at the shoulder. Like modern pigs, these animals were omnivores, but leaned toward carrion and live prey such as large ungulates. Hominoidea (apes) were diverse in the Miocene. Most modern mammal and bird families had appeared by the end of the Miocene.

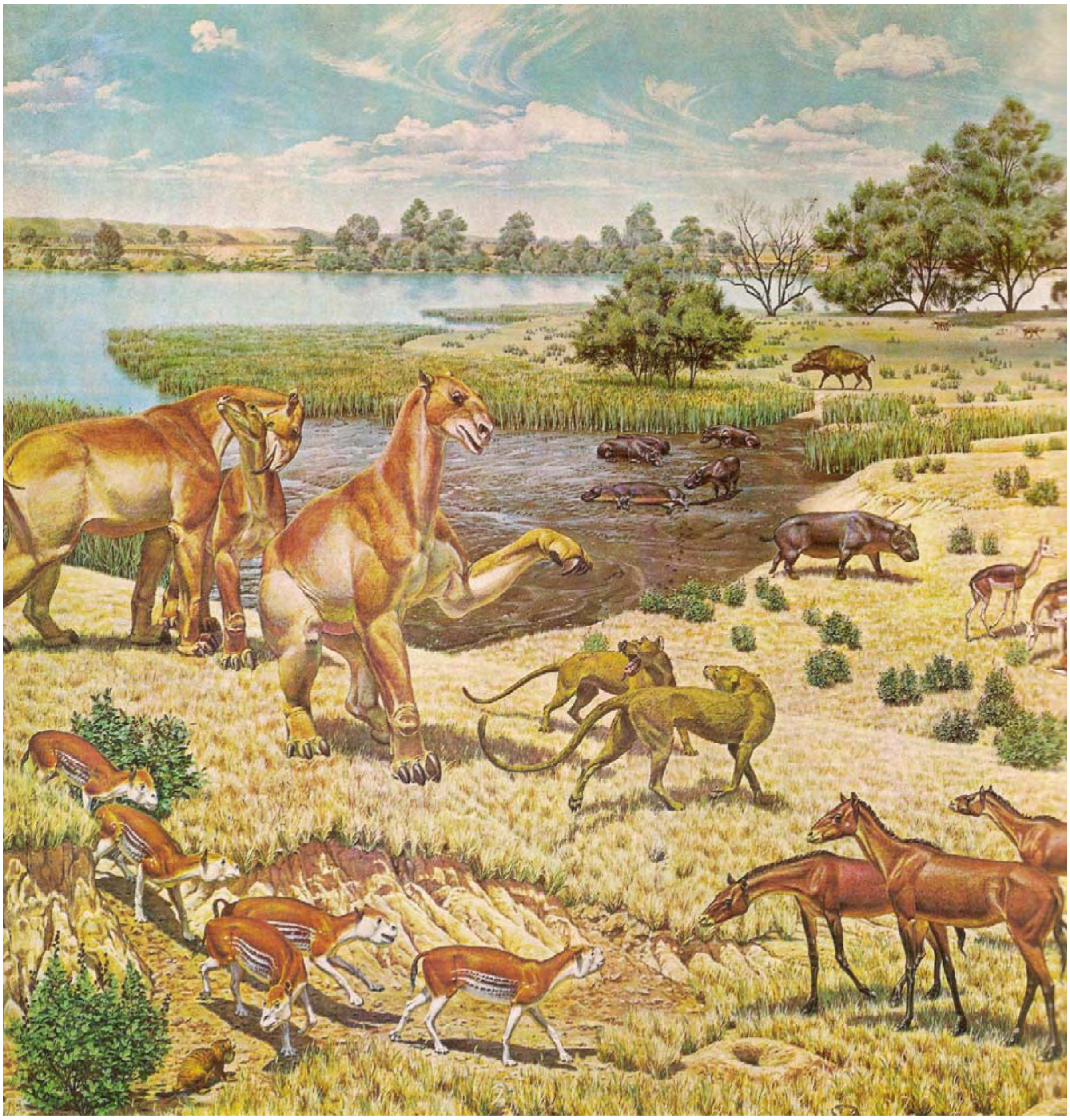

Figure 7.11: Depiction of the Miocene fauna of North America.
(Wikipedia 'Miocene;' Attribution: Jay Matternes)

In the oceans, whales and sharks were abundant and diverse. Kelp forests supported diverse vertebrate and invertebrate assemblages. In South America, freshwater habitats contained a variety of crocodilians, including the 12-meter long *Mourasuchus* which, despite its large size, probably collected food in a filter-feeding manner. *Mourasuchus* would sweep its shovel-like jaws through the water, and then use its rows of numerous small teeth to trap the prey as the water was forced out. South American waters were also home to *Megapiranha*, a now-extinct piranha that reached lengths of almost a meter. A series of extinctions, known as the Middle Miocene disruption, occurred around 14.8 to 14.5 MYA, probably as a result of a dramatic cooling period. The Miocene Epoch ended, and the Pliocene began, about 5.3 MYA.

During the Pliocene, the continents continued to drift to positions very close to their modern day configuration. A major geological event during the Pliocene was the formation of the Isthmus of Panama, which was completed about 3 MYA. This event would have dramatic ramifications both climatically, and in terms of the Earth's biota, particularly that of South America. Lowering ocean levels would also expose the land bridge connection between North America and Asia. The Mediterranean Sea would form as a result of the joining of Africa and Europe.

Climatically, the Pliocene continued to become cooler, drier, and more seasonal, though temperatures were still slightly warmer than today's. There were several possible reasons for this cooling trend. The formation of the Isthmus of Panama disrupted the flow of warm equatorial ocean currents, leading to the cooling of the now isolated Atlantic Ocean by waters from the Antarctic and Arctic regions. Also, formation of mountain chains such as the Rocky Mountains of western North America may have disrupted jet stream flow, leading to cooler temperatures. Finally, there was a decrease in atmospheric CO_2 that may have lessened the greenhouse effect during the Pliocene. Increased glaciation could have led to further cooling by increasing the Earth's albedo. These changing climatic conditions led to further increases in grasslands, savannas, and deserts, increasing deciduous and coniferous forests, and reduction of tropical forests. Marine and terrestrial faunas were increasingly similar to modern-day forms. In Africa, ungulates were abundant, and primates continued to diversify. The Tribe Hominini arrived on the scene, and this lineage would eventually lead to humans and our close relatives. Snakes continued to evolve, and the first rattlesnakes appeared.

The most dramatic changes in biogeographical patterns occurred as a result of the "**Great American Interchange**" associated with the formation of the Isthmus of Panama. This land bridge allowed two-way dispersal of flora and fauna between continents. Before this connection formed, South America had been isolated for tens of millions of years since its separation from Antarctica. In its isolation South America evolved a biota rivaling that of Australia in its uniqueness. South America was home to huge xenarthrans such as ground sloths and armadillo-like glyptodonts. There was also a unique ungulate fauna that included the camel-like *Macrauchenia* and other members of the Order Litopterna, as well as a diverse group of ungulates known as the notoungulates. Caviomorph rodents flourished as well. This group includes the capybara, porcupine, and guinea pig, as well as the largest of all rodents, the extinct *Josephoartigasia monesi*. This giant weighed in at one ton, about 20 times the weight of today's largest rodent, the capybara. Extinct predators include the aforementioned terror birds, as well as the cougar-like *Thylacosmilus*. With its oversized canines, this marsupial "cat" showed convergent evolution with the later saber-toothed placental cats (*Smilodon*) of the Pleistocene. In both cases, the bite was probably relatively weak compared to that of similarly-sized modern-day predatory cats such as the leopard. But the strong cervical vertebrae and powerful neck muscles give away these saber-tooths' *modus operandi* – rather than biting, the large canines were used in a powerful stabbing motion.

Before the formation of the Panamanian land bridge, South America was home to a rich variety of rodent-, rabbit-, cat-, and bear-like marsupials that shared the continent with their placental cousins for millions of years. But significant change would come in the form of the Great American Interchange made possible by the land bridge. This interchange has been the subject of detailed analyses, particularly by paleontologists Larry Marshall and David Webb, who wrote many groundbreaking papers on the subject in the 1970s and 80s. Based on Marshall and Webb's 1982 paper in the journal *Science*, 24 North American genera dispersed southward, whereas only 12 South American genera dispersed northward. These numbers represented similar proportions of the numbers of genera of the respective continents at that time. Immigrants from North America included small and medium-sized mammals such as rodents, rabbits, shrews, raccoons, and foxes, but also some larger mammals such as bears, horses, llamas, and mastodons (Fig. 7.12). The short-faced bear, *Arctotherium*, may have been the world's largest terrestrial carnivorous mammal, weighing in at about 1.5 tons. In the other direction, opossums, porcupines, armadillos, glyptodonts, the notoungulate *Mixotoxodon*, and ground sloths were among the dispersers.

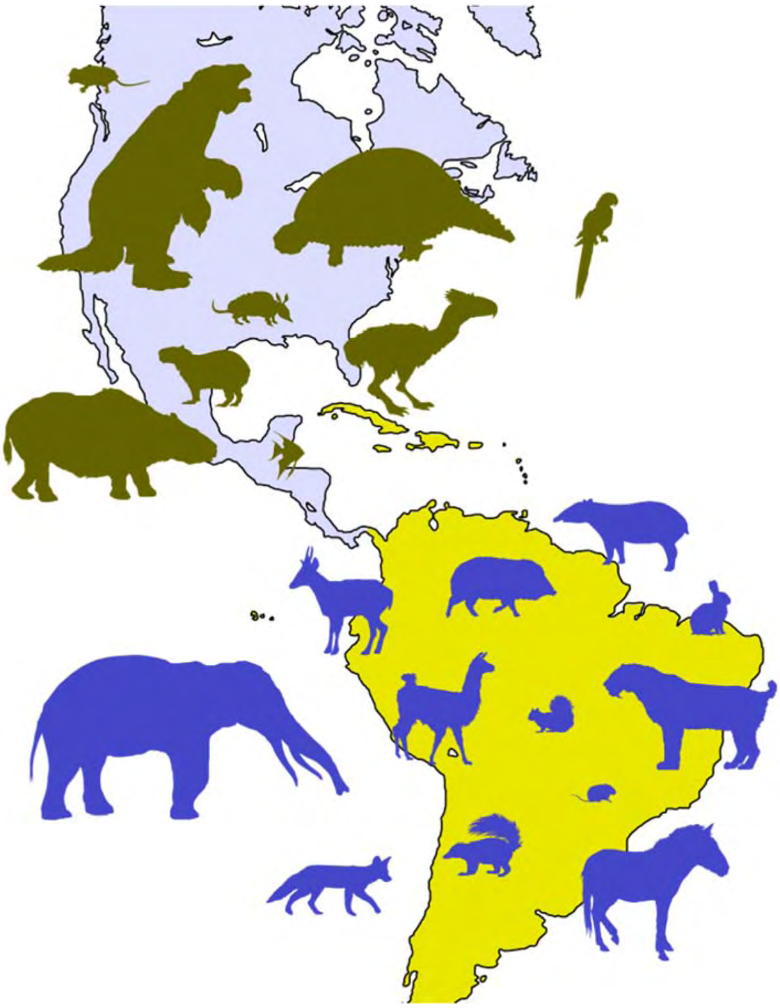

Figure 7.12: Examples of migrant species in the Americas after the formation of the Isthmus of Panama. Olive green silhouettes denote North American species with South American ancestors; blue silhouettes denote South American species of North American origin. (Wikipedia 'Pliocene;' Attribution: Woudloper)

By any measure, the southward dispersers from North America were more successful. Dispersing mammals from North America left about 85 descendent genera in South America; this accounts for about 50% of the total present-day mammal genera of South America. In present-day North America, on the other hand, only 29 genera, or 21% of the total, are descended from South American dispersers. This result is due to a combination of two interrelated factors – greater adaptive radiation of North American dispersers in South America, and higher extinction rates of native South American genera. In South America, nearly all of the once diverse marsupial fauna went extinct; only the "monito del monte" (a tiny, arboreal, mouse-like marsupial), the order Paucituberculata (several species of shrew- or rat-like marsupials known as "shrew opossums"), and the true opossums (Family Didelphidae) remain. The latter group is widespread, and the Virginia opossum (*Didelphis virginiana*) is even found throughout much of North America. But the monito del monte is found only in the highlands of southwestern South America (Chile and Argentina), and the shrew opossums only in the Andes Mountains.

Other South American mammals suffered as well in the aftermath of the Great American Interchange. Invasion by North American saber-toothed cats, bears, and various canids led to the demise of many large South American herbivores. All litopterns except *Macrauchenia* and the closely related *Xenorhinotherium* died out, as did many notoungulates. Many South American carnivores lost out in competition with the North American invaders as well. Phorusrhacids and sparassodonts were displaced. South American dispersers moving north had much less success, although the Virginia opossum, nine-banded armadillo (*Dasypus novemcinctus*), and North American porcupine (*Erethizon dorsatum*) have survived and flourished. Others, such as glyptodonts, giant sloths, and phorusrhacids made it to North America, but subsequently went extinct.

There have been several explanations proposed for this asymmetrical success rate. One of these explanations rests on the long period of isolation that South America underwent after separation from Antarctica. As we saw when we discussed island biogeography (Chapter 6), it is well known that isolated species on small islands are often at a great disadvantage when faced with newly introduced predators or competitors from the mainland. The same principle appears to apply, albeit to a lesser extent, to larger isolated landmasses as well. During the Cenozoic, North America was linked to Eurasia via the Bering Land Bridge, and Africa was connected to Eurasia as well. This meant that there was a vast, contiguous land area containing a great diversity of species competing with each other, and preying on and evading each other, all in a wide variety of different habitats and climatic conditions. Under these conditions, the Northern Hemisphere's evolutionary arms race produced swifter, more intelligent, and more competitive species. South America, on the other hand, was a smaller landmass that had been isolated for millions of years. During South America's isolation, its species interacted with fewer competitors and predators, and there were far fewer individuals and much smaller gene pools to provide the raw material of evolutionary innovation. Thus, during and in the aftermath of the Great American Interchange, South American mammals were at a competitive disadvantage in their newly-established interactions with their North American counterparts.

But there were other factors at play as well. To begin with, climate favored the North American dispersers. The climate of Central America is more similar to that of South America (tropical) than to North America. So dispersers moving south into South America would have of necessity already been well adapted to the tropical climate, whereas dispersers moving north would have encountered very different, drier and cooler conditions in southern and central Mexico. Also, a cooling climate at the time was producing a more arid, savanna environment in the region, which favored the North American species at the expense of the South American species, which were more adapted to tropical closed forest environments. It appears that lower competitiveness or intelligence among the South American groups does not tell the complete story of the Great American Interchange. About 2.6 MYA, the Pliocene ended and the Quaternary Period and Pleistocene Epoch began.

Quaternary period

The Quaternary Period is divided into two Epochs: the Pleistocene, from 2.6 MYA to 11,700 years ago, and the Holocene, from 11,700 years ago to the present. During the Pleistocene, the continents were in essentially their present-day positions. This epoch was characterized by repeated cycles of glaciation. At least 11 major glacial events occurred in the Pleistocene, punctuated by relatively mild periods, or "interglacials," which are warm and extended enough for temperate vegetation to exist. A shorter, cooler event, in which conditions might support boreal taxa, is known as an "interstadial." Several factors drive the process of glaciation. Important among these are the development of ice sheets at the poles and in Greenland. These ice sheets have higher albedo, or reflectivity, than the Earth as a whole. This means that, when these ice sheets are present, more of the incoming solar radiation is reflected rather than retained, leading to planetary cooling and a potential ice age.

But how can the fairly regular pattern of cold and warmer periods during an ice age be explained? An explanation, now widely accepted, for this pattern was proposed in the 1930s by **Milutin Milanković** (1879–1958; Fig. 7.13), a Serbian mathematician, climatologist, and geophysicist. Interestingly, Milanković apparently began some of the early work on his theory while he was imprisoned. He was on honeymoon with his new bride in Austro-Hungary near the outbreak of World War I. Tensions were high between Austro-Hungary and Serbia, and, being a Serbian citizen, Milanković was arrested. However, a friend arranged for Milanković to serve his captivity in Budapest so he could continue his work.

Figure 7.13: Milutin Milanković, Serbian scientist who explained the cyclical pattern of the Earth's climate using "Milanković cycles". (Wikipedia 'Milutin Milanković;' Attribution: Source unknown)

Milanković's theory rested on three factors: the Earth's orbital eccentricity (the elliptical, rather than circular, shape of the Earth's orbit around the sun); the tilt of the Earth's axis; and the variation in orientation, or "wobble," of the Earth's axis. All of these factors affect the amount of solar energy reaching the Earth and, since these three phenomena all follow predictable patterns, Milanković reasoned that combining them should make it possible to predict climate change patterns. More recent research and evidence have largely verified and improved on Milanković's theory. A particularly important paper in this area was published by James Hays, John Imbrie, and Nicholas Shackleton in 1976 in the journal *Science*. This paper confirmed that these "Milanković cycles" can be detected in marine sediments, and played a great role in bringing Milanković's theory to the forefront.

The predominately cold climate, dramatic climate changes, and advancing/receding glaciers had dramatic impacts on Pleistocene flora and fauna. During ice sheet expansion, many regions that are now temperate forests were either occupied by tundra vegetation, or even glaciated. During interglacials, the reverse was true. In each case, relatively small refugia provided environments in which isolated groups of species could survive. For instance, some high altitude locations remain tundra during interglacials, allowing organisms adapted to such conditions to survive in isolated pockets.

During the Pleistocene, terrestrial and marine faunas were similar to those of the present day in general, but the epoch did play host to an amazing group of animals known as the Pleistocene megafauna. Many of these were holdovers from the Neogene. The Pleistocene megafauna (Fig. 7.14) varied somewhat from continent to continent, but included, among others, giant sloths, the American lion (the largest subspecies of lion), mammoths and mastodons, glyptodonts, saber-toothed cats, cave bears, short-faced bears, three now-extinct species of bison, wooly rhinos, and the Irish elk, with its massive antlers. Large birds were present as well, including the now-extinct giant condor, *Aiolornis incredibilis*. With a 5 m wingspan, this was one of the largest known flight-capable birds.

Figure 7.14: Pleistocene fauna of what is now northern Spain.
(Wikipedia 'Pleistocene;' Attribution: Mauricio Antón, Public Library of Science)

Australia was home to a variety of large marsupials, including the "marsupial lion," *Thylacoleo carnifex*, and giant 3-meter long wombats (*Diprotodon*). Three-meter tall flightless birds in the Family Dromornithidae also graced the Australian landscape; with their powerful crushing beaks, these birds may have filled a predator/scavenger niche similar to that occupied by today's hyenas. The Pleistocene fauna of Australia also included giant snakes in the genus *Wonambi*. These snakes reached up to 6 m in length. They were probably predators that ambushed such prey as kangaroos and wallabies, and killed them through constriction. These snakes achieved mythical status in aboriginal cultures. All of the megafauna species described above are now extinct, probably due to a great extent to the spread of another species that would begin to assert its dominance in the Pleistocene, *Homo sapiens*. Much of the megafaunal extinctions took place during the transition from the Pleistocene to the Holocene Epoch. The Holocene epoch will be discussed in the next chapter, which addresses human evolution and biogeography.

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8 HUMAN EVOLUTION AND BIOGEOGRAPHY

Your goals for this chapter are to learn about:

- The major species comprising the human evolutionary tree
- Early agriculture and animal domestication
- Possible geographic factors that underlie human inequality
- The Anthropocene
- Measuring human impacts
- Extinctions
- The Columbian Exchange
- Exotic and invasive species
- Anthropogenic climate change

8.1 INTRODUCTION

Modern humans and our precursors have existed for millions of years. From our humble beginnings after splitting from the chimpanzees in Africa roughly 7 MYA, the human lineage has produced a highly branched evolutionary tree of more than 2 dozen species. But now only one remains: *Homo sapiens*, a species that has developed the capability to transform the world. In this chapter, we will briefly review the major events in the history of human evolution and biogeography, and discuss the ecological impacts that *H. sapiens* have had on the planet's biota.

8.2 HUMAN EVOLUTION

Understandably, there is great interest in our own branch of the evolutionary tree, and the study of human evolution is a vibrant and exciting field. Our understanding of human phylogeny has historically been based primarily on the fossil record, but more recently, molecular biology and DNA analysis have played increasingly important roles. Even so, reconstruction of human phylogeny is often based on incomplete evidence. Consequently, our views of human phylogeny are frequently being revised as more evidence comes to light. Figure 8.1 shows a phylogeny of humans that includes the genera and species discussed in this chapter. Temporal ranges given for periods when human ancestors lived are, of necessity, rough estimates.

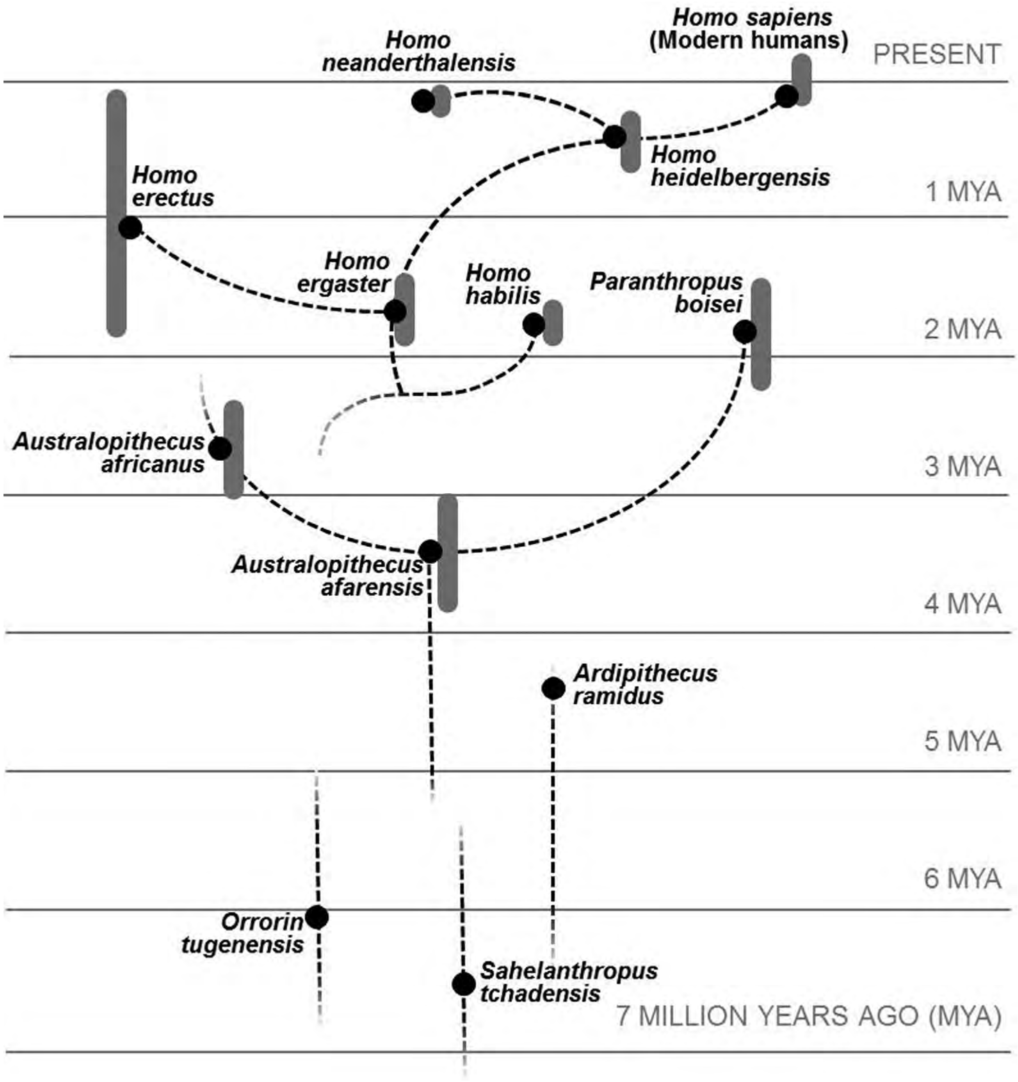
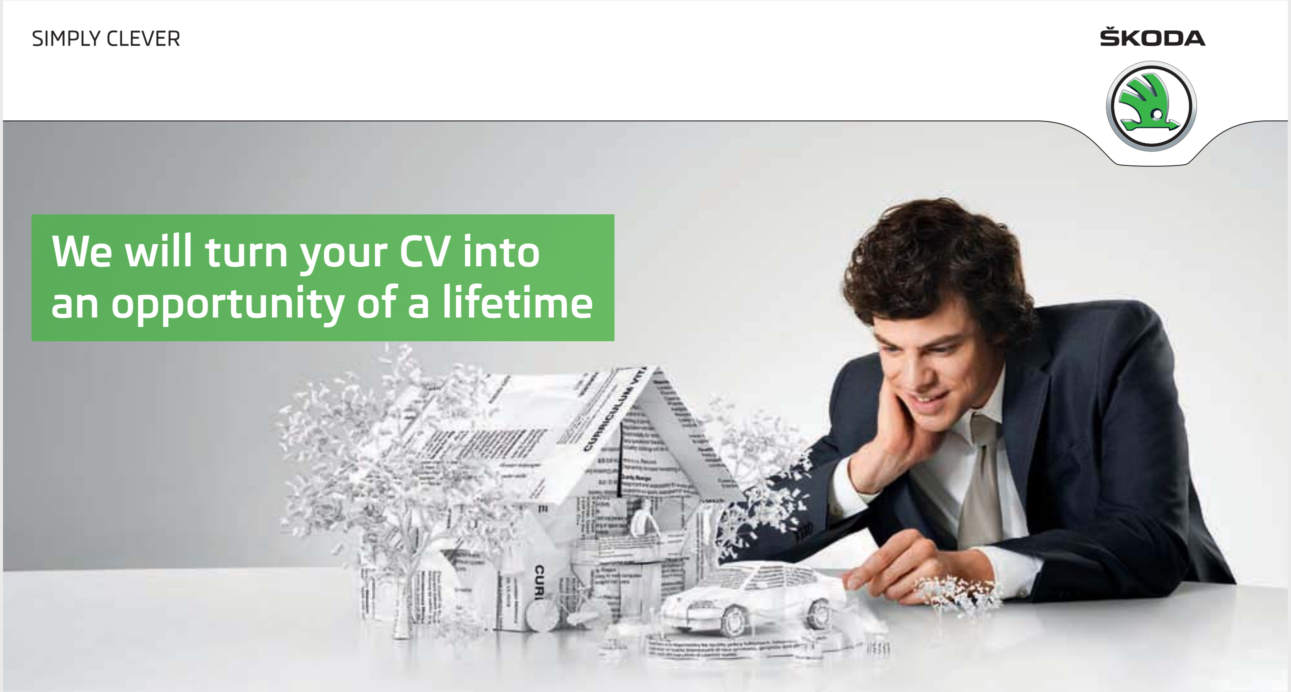


Figure 8.1: A phylogeny of humans, focusing on groups discussed in this chapter. (Modified from http://www.amnh.org/education/resources/rfl/web/hhoguide/family-tree.html; Attribution: Shawn Meagher, Western Illinois University)

Based on available evidence, *H. sapiens* ("wise man") arose about 200,000 years ago in Africa. *Homo sapiens* is the most recent in a long lineage that may have begun around 7 MYA ago with *Sahelanthropus tchadensis*, possibly the common ancestor of humans and the genus *Pan* (chimpanzees and bonobos), although this is far from settled. In *S. tchadensis* the foramen magnum (the opening of the skull where the spinal cord exits) is located underneath the skull, indicative of bipedal locomotion, although this interpretation is under dispute. In apes, this opening is located more posteriorly, reflecting a more quadrupedal locomotion. The Genus *Homo* is in only genus in the subtribe Hominina of the tribe Hominini, which, in addition, includes the subtribes Australopithicina (*Australopithecus* and closely related genera) and Panina (with the one genus, *Pan*). The Hominini that arose after separation from the chimpanzees (i.e., the subtribes Hominina and Australopithicina) are collectively referred to as hominins, or the "human clade."

Orrorin tugenensis is a contender along with *S. tchadensis* for the title of earliest human. *Orrorin tugenensis* had microdont dentition (small teeth) reminiscent of humans, but with canines that are ape-like, but reduced. Specimens of this species have been dated from around 6 MYA. *Orrorin tugenensis* was probably a tree-climber, but also perhaps bipedal to some extent. If *O. tugenensis* is indeed an early part of the human lineage, then the Australopithecina, which occurred later, were side branches from this main human line. But again, this is under debate.

Genera of Australopithecina include *Ardipithecus* (6.0 to 4.4 MYA), *Australopithecus* (4 to 2 MYA), and *Paranthropus* (2.7 to 1.2 MYA). The best known species in the genus *Ardipithecus*, *A. ramidus*, was about 1.2 m tall. Based on pelvis and limb structure, *Ardipithecus* may have been facultatively bipedal, that is, bipedal when moving along the ground, but using all four limbs when moving in the trees. Its bipedal locomotion was primitive and inefficient compared to later hominins, and its brain size was only about 300–350 cm^3, or about 25 to 30% that of modern *H. sapiens*.



The genus *Australopithecus* appeared later, around 4 MYA, and over the course of a couple of million years would be represented by several species. *Australopithecus afarensis* (Fig. 8.2) is probably the best known species, and is represented in the fossil record by the well-known partial skeleton named "Lucy." Sexual dimorphism in *Australopithecus* was substantial; males were about 1.5 m tall, and females about a half meter shorter. Anatomical evidence and footprints preserved in volcanic ash in Tanzania indicate that *Australopithecus* were bipedal. Compared with *A. afarensis*, *Australopithecus africanus* appears to have pelvic structure better suited for efficient bipedalism. *Australopithecus* brain size was significantly greater than that of *Ardipithecus*, but still relatively small, measuring about 425 cm^3, or about 35% that of modern humans. The small brain coupled with bipedal locomotion has cast doubt on the long-held view that increased brain size preceded bipedalism in human evolution. Based on dental microwear and trace element studies, *Australopithecus* apparently ate primarily fruits, vegetables, and tubers, probably supplemented with meat. Fossils of butchered animal bones associated with *Australopithecus* sites also suggest meat-eating, as well as early tool use, dating about 3.4 MYA.

Figure 8.2: A reconstruction of a female *Australopithecus afarensis*. (Wikipedia '*Australopithecus afarensis*;' Source unknown)

Paranthropus are also known as “robust austalopithecines.” They probably descended from *Australopithecus*. Some paleontologists think that *A. africanus* evolved into *Paranthropus*, and *Paranthropus* species are sometimes included in the genus *Australopithecus*. *Paranthropus* were around 1.3 m tall, with males somewhat taller and larger than females. *Paranthropus* were generally stouter than *Australopithecus*, and had more robust cranial anatomy. The brain of *Paranthropus* was larger than that of *Australopithecus*. There is evidence that *Paranthropus* used tools, perhaps to a greater extent than did *Australopithecus*. Like *Australopithecus*, *Paranthropus* was bipedal. The diet of *Paranthropus boisei* appears to have been based to a great extent on C_4 plants such as grasses and sedges, which would have been plentiful in the open savanna habitats in which *P. boisei* lived. *Paranthropus* overlapped with the earliest members of the genus *Homo*, *Homo habilis*, and may have coexisted with other *Homo* species as well. But *Paranthropus* went extinct about 1.2 MYA, whereas *Homo* survived and flourished. Perhaps the more specialized diet and less advanced tool use of *Paranthropus* led to their demise.

The genus *Homo* first appeared in Africa about 2.1 MYA, with *Homo habilis* (Fig. 8.3) as its earliest representative. Among species in the genus *Homo*, *H. habilis* is the least similar to modern humans, with some ape-like features such as relatively long arms and forward-jutting jaws. *Homo habilis* were small compared to later *Homo*, with a height of about 1.25 m. Some paleontologists have suggested that *H. habilis* is more appropriately included in the genus *Australopithecus*. However, *H. habilis* had a brain roughly 50% larger than *Australopithecus*, though still less than half that of modern humans. *Homo habilis* used stone flake tools, probably for cutting meat from carrion rather than for active hunting or defense. Fossil evidence indicates that *H. habilis* frequently fell victim to large predators such as the saber-toothed cat, *Dinofelis*. *Homo habilis* was probably not the first human tool user; evidence suggests that *Australopithecus* had used tools previously, and *Paranthropus* used tools as well. But *H. habilis* may have been the first tool makers.

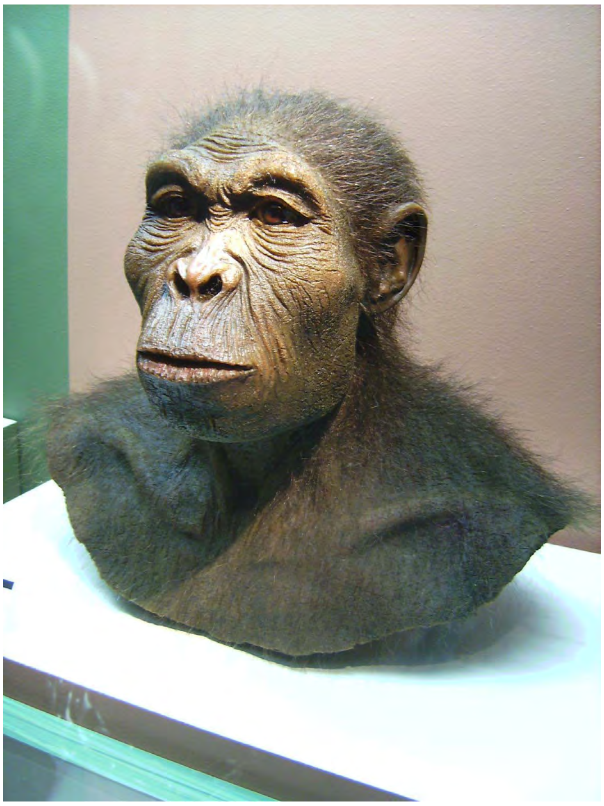


Figure 8.3: A reconstruction of *Homo habilis*. (Wikipedia '*Homo habilis*;' Attribution: Photographed at Westfälisches Museum für Archäologie, Herne, by Lillyundfreya)

Homo habilis persisted until about 1.5 MYA, and thus coexisted with another human species, *Homo erectus* (Fig. 8.4), which first appeared about 1.9 MYA. The relationship between these two species is still being debated. Some paleontologists consider the two species to be separate lines from a common ancestor, but others suggest that *H. erectus* was derived from an isolated population of *H. habilis*, and the remainder of the latter species coexisted with *H. erectus* for a few hundred thousand years. With an average height of about 1.7 m, *H. erectus* was substantially taller than *H. habilis*, although there was a great deal of height and size variation in *H. erectus*.

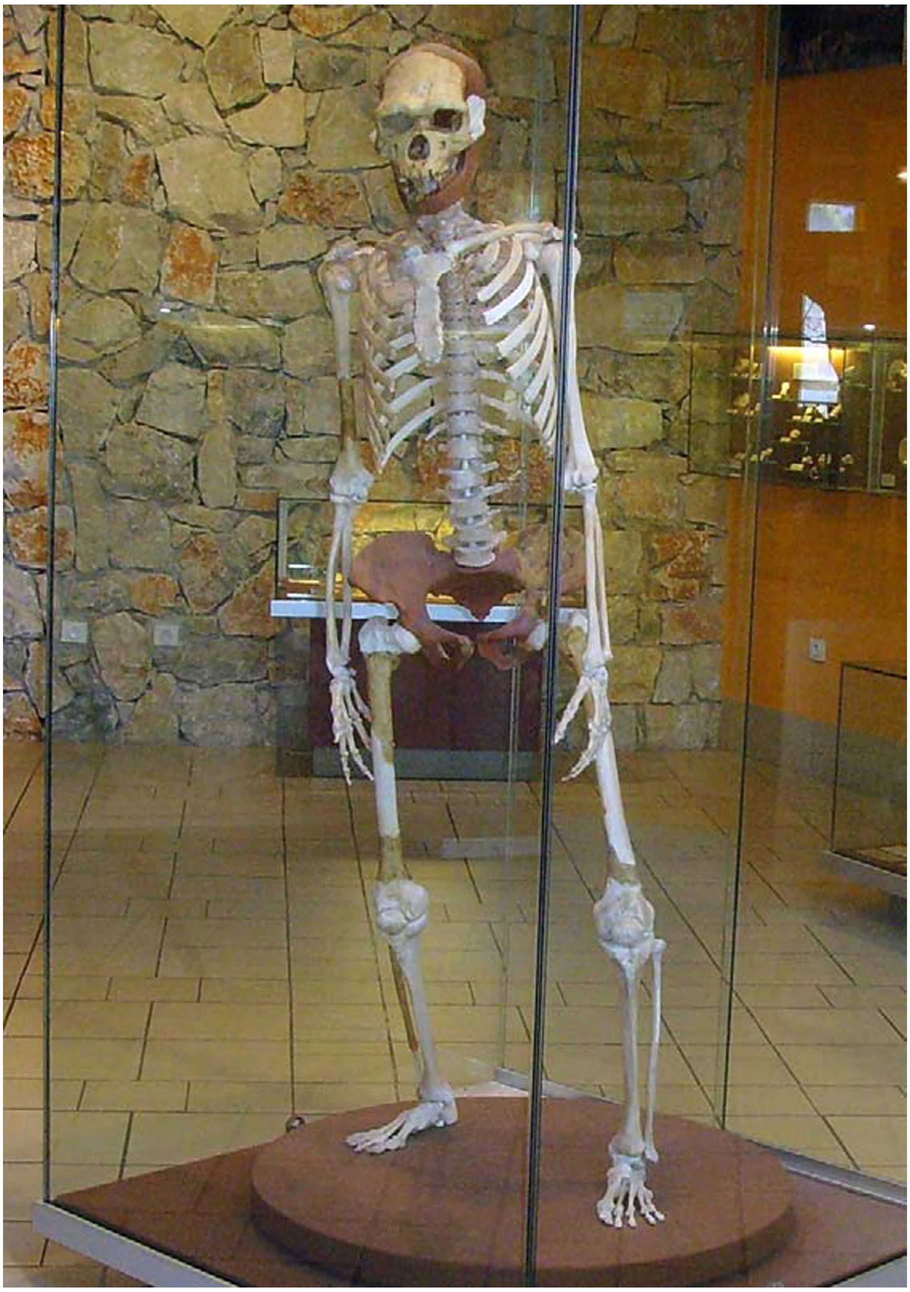


Figure 8.4: A reconstruction of a *Homo erectus* skeleton from Tautavel, France. (Wikipedia '*Homo erectus*;' Attribution: Gerbil)

Compared to *H. habilis*, *H. erectus* had greater brain capacity as well, about ¾ the capacity of modern humans. The larger body size and brains of *H. erectus* required greater energy inputs, and meat, being more easily digestible, played a greater role in the diet of *H. erectus*. Tool making and use became more sophisticated than that found in *H. habilis*. However, some paleontologists have recently suggested that several species of *Homo* that existed around 1.8 MYA, including *H. habilis*, *Homo rudolfensis*, *Homo ergaster*, and *H. erectus*, in reality represent variation within a single species, best referred to as *H. erectus*. *Homo erectus* has the distinction of being the longest surviving species of *Homo*, existing for over a million years before becoming extinct. In comparison, *H. sapiens* have existed for roughly 200,000 years. During their time, *H. erectus* became quite widespread; fossils have been found in Africa, Eurasia, Indonesia, China, and Southeast Asia.

Homo heidelbergensis (Fig. 8.5) is a relatively recent human species, first appearing about 600,000 years ago. *Homo heidelbergensis* were larger in both body size (about 1.75 m and 1.57 m in height for males and females, respectively) and brain case volume (1100 to 1400 cm^3) than previous *Homo* species. These measurements substantially overlapped the ranges of modern humans in both respects. *Homo heidelbergensis* were the first humans to inhabit cold climates in substantial numbers, and their compact body forms were an adaptation that increased heat retention due to reduction in surface area-to-volume ratio. *Homo heidelbergensis* were innovative in many ways. They were the first humans to use controlled fire, and also used wooden spears to hunt large game. They were also the first to build shelters, using wood and rocks.

Figure 8.5: A reconstruction of *Homo heidelbergensis*. (Wikipedia '*Homo heidelbergensis*;' Attribution: Jose Luis Martinez Alvarez from Asturias, España)

It is thought that separate branches of the *H. heidelbergensis* lineage gave rise to *H. sapiens* as well as "Neanderthal man." Some paleontologists consider Neanderthals to be a subspecies of *H. sapiens*, *Homo sapiens neanderthalensis*. However, most consider them to be a separate species, *Homo neanderthalensis* (Fig. 8.6). There was substantial overlap between *H. neanderthalensis* and *H. sapiens* temporally, and the two species coexisted in Europe for about 5,000 years after the arrival of *H. sapiens* there. In terms of body size, *H. neanderthalensis* was similar to *H. heidelbergensis*, but somewhat shorter and stouter, again reflecting adaption for heat conservation in cold climates. *Homo neanderthalensis* had large brains; as large as or larger than that of modern *H. sapiens*. *H. neanderthalensis* took the behaviors found in *H. heidelbergensis* to new levels of sophistication. *Homo neanderthalensis* made and used a variety of complex tools; they constructed shelters, made clothing, and engaged in symbolic behaviors such as burying their dead and marking graves with objects such as flowers. *Homo neanderthalensis* were accomplished hunters and, like *H. heidelbergensis*, incorporated meat into their diet, particularly during the winter when plant foods were scarce. The diet of *H. neanderthalensis* often included large, dangerous game; frequent bone fractures in *H. neanderthalensis* attest to this.

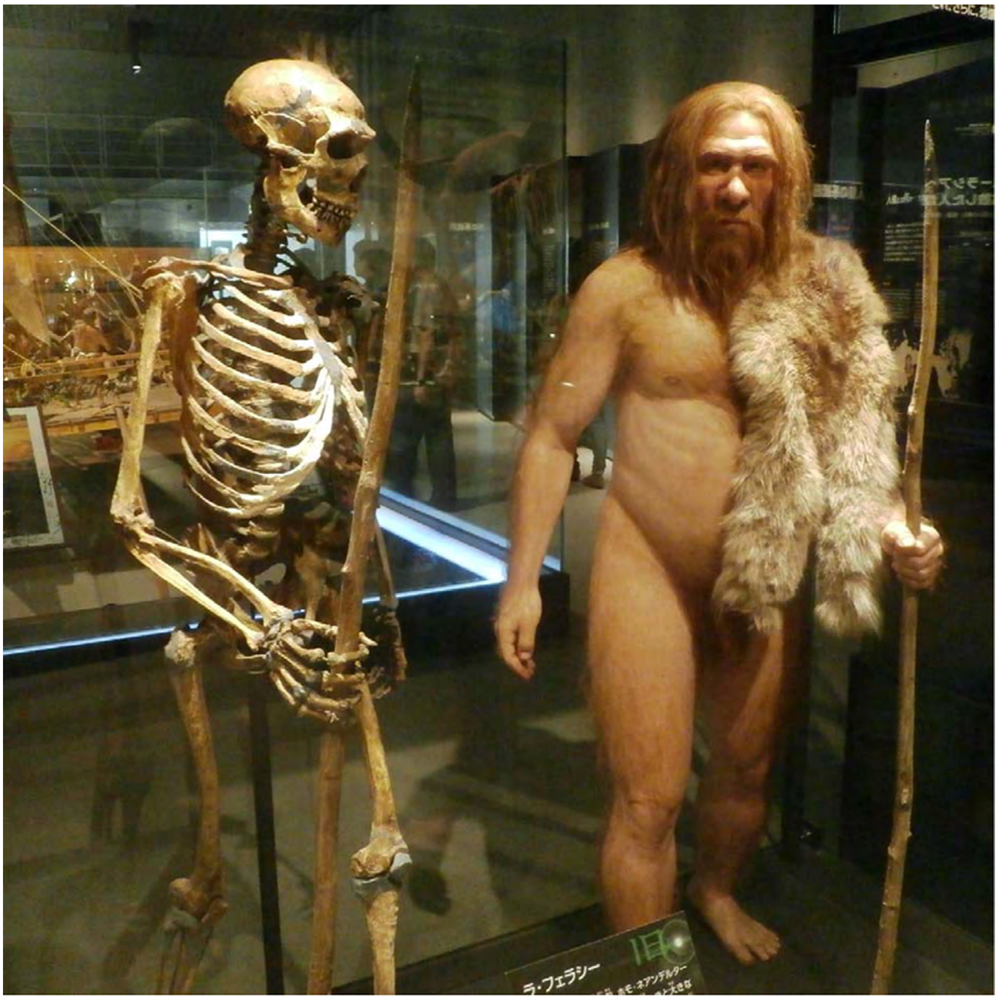


Figure 8.6: Skeleton and reconstruction of a Neanderthal man. (Wikipedia 'Neanderthal;' Attribution: Photaro)

Homo neanderthalensis disappeared about 30,000 years ago, soon after the arrival of *H. sapiens* in Europe. What caused the demise of *H. neanderthalensis*? Several hypotheses have been proposed, some of which invoke direct or indirect interactions with *H. sapiens*. One suggestion is that *H. neanderthalensis* was unable to compete for food and resources effectively with *H. sapiens*, perhaps because their short, stout limbs did not allow *H. neanderthalensis* to move as effectively as *H. sapiens*. UCLA biologist Jared Diamond has proposed that anatomical factors limited the ability of *H. neanderthalensis* to produce complex speech and communicate effectively in comparison to *H. sapiens*. Diamond has also suggested that direct conflict between the two species could have resulted in violence and genocide of *H. neanderthalensis*. Some have also suggested that *H. sapiens* may have hunted and eaten *H. neanderthalensis*. *Homo sapiens* may have also contributed to the extinction of *H. neanderthalensis* by transmitting pathogens or parasites which were new to *H. neanderthalensis* and to which *H. neanderthalensis* therefore had little immunity. It is also possible that *H. neanderthalensis* was poorly equipped to survive climate change that was occurring at the time. Certainly these potential causes are not mutually exclusive, and it is quite possible that a combination of these or other factors may have led to the extinction of *H. neanderthalensis*. However, there is some genetic evidence of interbreeding between *H. neanderthalensis* and *H. sapiens*, meaning that *H. neanderthalensis* genes may still persist in modern humans. *Homo neanderthalensis* and *H. heidelbergensis*, along with another species, *Homo rhodesiensis*, are generally referred to as "archaic humans," anatomically distinct from *H. sapiens*.

The origins of modern *H. sapiens* have been debated for decades, but recent evidence supports the "recent single-origin hypothesis" (otherwise known as the "out of Africa" hypothesis). In this view, supported by genetic and fossil evidence, *H. sapiens* evolved from archaic humans solely in Africa between 200,000 and 60,000 years ago. One group of *H. sapiens* left Africa between 125,000 and 60,000 years ago, and over time displaced other species in the genus *Homo* in other geographic locations. A competing hypothesis, the "multiregional hypothesis," asserts that one continuous human species, which includes archaic humans as well as *H. sapiens*, evolved throughout the world into the various geographic populations of *H. sapiens*. This hypothesis currently has much less support in the paleoanthropological community than does the recent single-origin hypothesis. By 30,000 years ago, *Homo sapiens* had spread from Africa to Europe, Asia, and the Australasian region. Approximately 15,000 years ago, during the late Wisconsinan Glaciation, low sea levels exposed the Bering Land Bridge, allowing colonization of the Americas from Asia.

About 13,000–12,000 years ago, the North American megafauna underwent large-scale extinctions, a pattern that had occurred during earlier time periods in other parts of the world. These extinctions may have had multiple causes. Climate change may have been an important factor. However, evidence suggests that, in several locations, these extinctions correlate closely with the arrival of humans, and the animals that went extinct were large herbivores or flightless birds that would likely have been the focus of human hunting. The idea that humans were responsible for megafaunal extinctions is known as the **Pleistocene overkill hypothesis**.

In addition to those species discussed in this section, the human clade has included numerous others that have entered and exited the human evolutionary stage over the last 7 million years. See the works listed at the end of the chapter for more information on these.

8.3 AGRICULTURE AND ANIMAL DOMESTICATION

One of the seminal events in human history is the domestication of certain animals and plants. In her recent paper on the relationship between humans and domesticated plants and animals, Melinda Zeder defined domestication as follows: “Domestication is a sustained multigenerational, mutualistic relationship in which one organism assumes a significant degree of influence over the reproduction and care of another organism in order to secure a more predictable supply of a resource of interest, and through which the partner organism gains advantage over individuals that remain outside this relationship, thereby benefitting and often increasing the fitness of both the domesticator and the target domesticate.” As this definition points out, domestication can be viewed as a mutualistic relationship, benefiting both partners. When we began to selectively breed particular individuals with certain traits, humans were, at a fundamental level, changing allele frequencies, and thus causing evolution, in food animals and plants. This process is now known as artificial selection. Thousands of years after the beginnings of domestication, Charles Darwin used this selection by humans as an analogy for how certain alleles are best able to survive and flourish in natural populations. He called this mechanism of evolution “natural selection.”

Somewhat surprisingly to many, human domestication of animals appears to have preceded plant domestication. There is disagreement on the exact date, but molecular genetic evidence suggests that the modern dog diverged from wolves at least 40,000 years ago which, presumably, corresponds to the timing of dog domestication. Other animals were domesticated much later. Pigs were domesticated roughly 15,000 years ago, sheep and goats about 12,000 years ago, and cattle around 10,000 to 11,000 years ago.

Until recently, the earliest evidence of plant domestication was thought to be about 10,000 to 12,000 years ago, in the form of wheat and barley cultivation. This took place in the area known as the “Fertile Crescent,” or Mesopotamia, the region that includes present-day Iraq, Kuwait, and parts of Iran, Turkey, and Syria (Fig. 8.7). However, recent studies done by Ainit Snir and colleagues at the Ohalo II site on the shore of the Sea of Galilee, Israel provide evidence of agricultural cultivation 23,000 years ago.

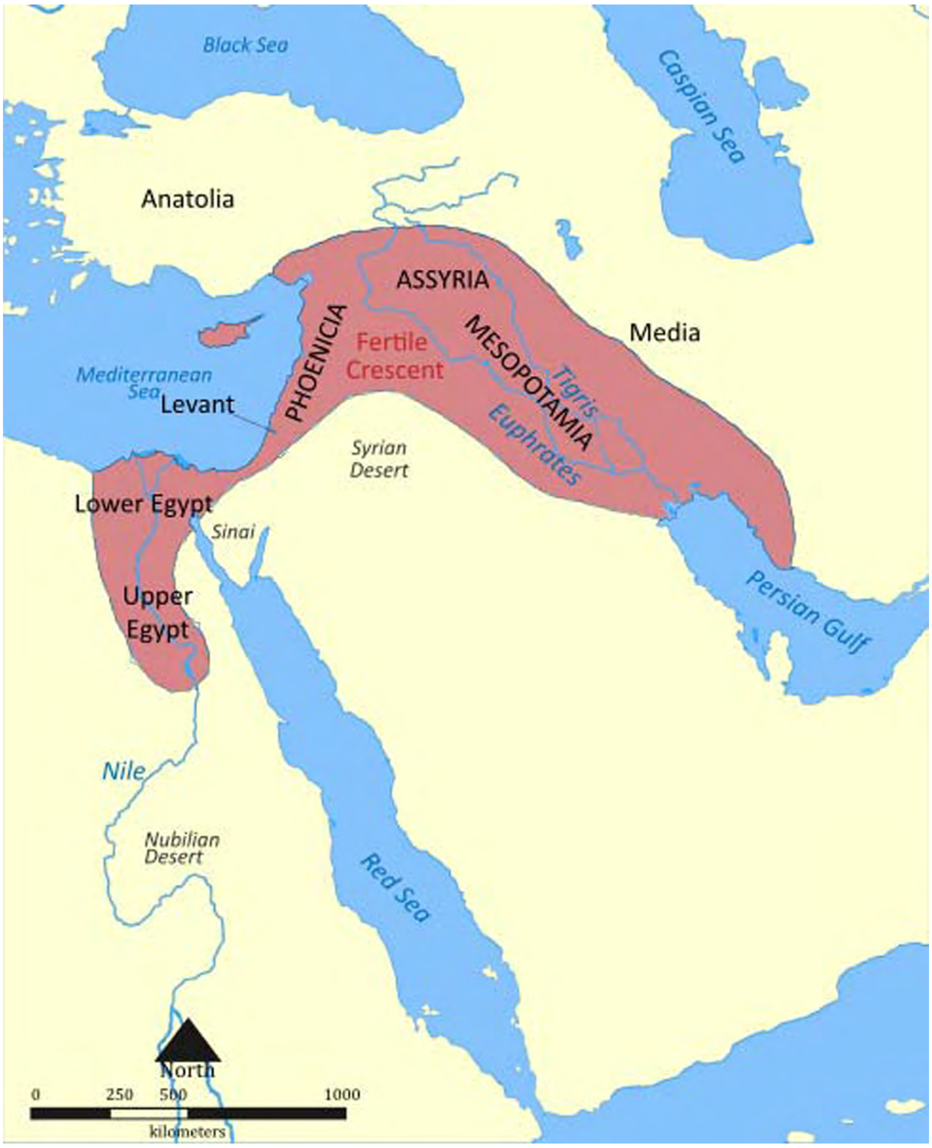


Figure 8.7: The Fertile Crescent. (Wikipedia 'Fertile Crescent;' Attribution: Nafsadh)

Many of our domesticated crops are the descendants of "weedy" species that colonize and grow well in disturbed soils. There is archaeological evidence from over 20,000 years ago of dough made from wild wheat, barley, and other grass species. It would have been a relatively small leap from taking advantage of these wild plants for food, to collecting and storing their seeds and then distributing them in soil previously disturbed for this purpose. Of course, variation in these plants meant that some had more desirable characteristics than others, and in time people learned to select for desirable traits. Other plants, such as pea, beans, alfalfa, and lentil were also domesticated in Mesopotamia. Centers of agriculture in other geographic regions developed a bit later – in China and the Americas beginning about 8,000 years ago, and Africa beginning about 7,000 years ago. However, there is some evidence of taro cultivation in Papua New Guinea almost 30,000 years ago, which would make this plant the first in the world to be cultivated.

The Agricultural Revolution, also known as the Neolithic Demographic Transition or the Neolithic Revolution, marked the transition of human populations from primarily scattered, hunter-gatherer societies to larger, more concentrated groups. This resulted from high agricultural productivity which produced enough food to support denser populations. Humans became less nomadic, and food surpluses made it possible for some people to work at non-food production activities, allowing better development of a variety of skills and new technologies. This led to a greater degree of specialization and to more organized, hierarchical societies.

The standard view is that the development of agriculture marked the beginning of a dramatic increase in the quality of human life. After all, plentiful food could now be had without all the hard work associated with hunting game and gathering plant foods. But recently, some have begun to question the accuracy of this view. Evidence now suggests that hunter-gatherers can meet their food requirements in fewer work hours than can agriculturalists. Agriculturalists' diets are also apparently less balanced and of lower quality than that of hunter-gatherers. Evidence shows that the stature of early Europeans after the change to agriculture decreased by 4 to 5 inches, from 5'10" (men) and 5'6" (women) to 5'5" and 5'1", respectively. Agriculture led to the development of vitamin deficiencies and teeth and bone problems. The close association with their domesticated animals also led to spread of diseases such as measles, influenza, smallpox, tapeworms, and *Trichinella* from animals to humans. Living a sedentary lifestyle in close proximity to their own feces also led to increased prevalence of parasites such as hookworms and other intestinal roundworms. Some have argued that the development of agriculture led to change from more egalitarian hunter-gatherer societies to highly stratified societies with concentration of wealth and power in a few hands, and high levels of inequality. The above deficiencies of agriculturally-based diets generally applied only to the poor and working class; the smaller number of wealthy, non-producing elites of the agricultural world were much healthier. Many of the problems associated with agrarian societies were reviewed by Jared Diamond in a 1987 *Discover* magazine article descriptively titled "The Worst Mistake in the History of the Human Race."

Whatever the costs and benefits of the agricultural way of life, the development of agriculture inevitably led to the displacement of hunter-gatherer societies. The large, concentrated populations associated with agrarian societies have, to a great extent, pushed their hunter-gather counterparts aside, and agriculture has overwhelmingly shaped the pathway that humanity has taken. That pathway has led to dramatic inequalities among human societies. In particular, Eurasian societies have come to gain hegemonic dominance over the modern world. Some ascribe this dominance to superior intelligence, talent, skill, or morality. But in his Pulitzer Prize-winning book *Guns, Germs, and Steel: The Fates of Human Societies*, Jared Diamond proposed a controversial new hypothesis to explain the roots of these inequalities. Diamond asserts that these inequalities are best explained by fundamental geographic and environmental differences rather than inherent Eurasian superiority.

Diamond argues that Eurasian success has been due, to a great extent, to the geographic "luck of the draw." With the rise of agriculture, Eurasians possessed early advantages in the availability of large numbers of plants and animals suitable for domestication. Eurasians had food plants such as wheat, barley, and edible legumes that were relatively nutrient rich, and easier to plant and cultivate than food plants in other regions of the world. Similarly, Eurasians had large numbers of animals such as sheep, goats, and cattle that had suitable behaviors, diets, and growth rates for domestication. Large mammals in particular are useful, not only for food, but in providing muscle power as beasts of burden. Diamond lists 14 large mammals worldwide that have been domesticated; of these all but two are descendants of wild species found in Eurasia, including the five most useful – sheep, goats, cows, pigs, and horses. Eurasia's long east-west axis was also advantageous in that it increased the likelihood of domesticated plants and animals from one location being well suited for other locations with similar latitudes and climates. These advantages in numbers of species suitable for domestication would translate into large advantages in food production, division of labor, long distance transport of materials, and economic and military superiority. This in turn would lead to the development of powerful nation-states and empires that would come to dominate most of the world.

The Eurasian advantage in animal domestication would have other ramifications as well. Their long, close association with domesticated animals meant that Eurasians had long exposure to a variety of parasites and pathogens, to which they evolved some immunity. When Europeans invaded the New World, they carried some of these pathogens with them. The indigenous people had never been exposed to these diseases, and had little immunity to them. The most devastating of these diseases was smallpox, but other diseases such as measles, cholera, and influenza caused many deaths as well. The number of indigenous people in the New World before the arrival of Europeans is unclear; estimates range from about 10 million to 100 million or more. After European contact, this number declined by 70 to 90%, mostly due to disease.

Diamond makes compelling arguments for the importance of geographic determinism in explaining the roots of human inequality. However, counterarguments can be made as well. There are exceptions to Diamond's examples; geographic locations where the conditions for agricultural development were excellent, but intensive agriculture never developed, and cultures that did develop efficient agriculture but still remained poor. There are many factors in addition to geography that can play a role in the development of societies, and the relationship between human success and their geographic setting is not a one-way street; humans are adaptable, and capable of altering their surroundings to suit their purposes.

8.4 THE ANTHROPOCENE

Since the advent of agriculture, *Homo sapiens* have altered the face of the Earth in a dramatic and accelerating fashion. The impact of human activities has been so great, that some scientists have asserted that we are now in a new geological epoch, the Anthropocene, although this has not yet been formally adopted by the geological community. The concept of an Anthropocene Epoch was popularized by atmospheric chemist Paul Crutzen and biologist Eugene Stoermer, and many scientists are using the term.

Debate has ensued regarding the official beginning of this epoch. Crutzen and Stoermer suggested the late 18th century, when James Watt's improvement of the steam engine was an important factor in the beginnings of the Industrial Revolution. Others have suggested the birth of agriculture as an appropriate beginning of the epoch. In order to define a geological time unit, geological stratigraphic material must contain a record of global-scale synchronous change. Several potential start dates/events have been proposed, ranging from the megafaunal extinctions that began roughly 50,000 years ago, to the origins of agriculture, to the presence of persistent industrial chemicals beginning about 1950.

In a recent paper in the prestigious journal *Nature*, Lewis and Maslin suggest that the above proposed start dates generally do not exhibit markers of sufficient global synchrony to be useful. They have proposed two potential start dates for the Anthropocene that do appear to meet this criterion – 1610 and 1964. The year 1610 marks a dramatic decrease in the amount of CO_2 in the atmosphere, and this appears to correspond to the precipitous (~ 90%) decline in the indigenous human population of the New World after the arrival of Europeans. This decline in the population of the New World, caused by disease, famine, and war, resulted in a significant decline in farming and the use of fire, which allowed regeneration of over 50 million ha of native vegetation. This increased vegetation in turn resulted in increased carbon uptake and the decline in global atmospheric CO_2. This date also corresponds to the beginnings of significant transoceanic movement of species. The 1964 date corresponds to peak levels of ^{14}C associated with radioactive fallout from nuclear bomb tests. With respect to early human evolution, an important question is "how did the geography of the Earth affect humans?" Now, an equally legitimate question is "how are humans affecting the Earth?" Regardless of the start date chosen for the beginning of the Anthropocene, there can be no doubt that *H. sapiens* is now the most important biological agent of change on Earth, and collectively we are changing the landscape, climate, and biodiversity of our planet in profound ways.

The sum total of human impacts on the Earth is a function of human population size and the degree of impact per individual. During the last 10,000 years, the human population has increased from a few million individuals to over 7 billion as of the year 2011. Population growth is expected to continue for decades, although at a decreasing rate, and is expected to reach 10 billion in the late 21st century. Thus, the human population has increased over 1,000-fold in the last 10,000 years. However, this tremendous growth has not been uniform over time. For most of this time period, growth was relatively slow, and there were even periods of population decline, such as the substantial dip in the 14th century due to the "black death." But in the last few centuries, the population has grown virtually exponentially; in the 20th century alone, the world human population increased by over 5 billion. This population growth has resulted in a corresponding increase in human impacts on the Earth.

However, population size is not the complete story. Individuals vary greatly in their capacity to change the Earth. One commonly used measure that depicts individual impacts on the Earth is the **ecological footprint**. This metric represents the area of productive land and sea that is required to supply the resources and absorb the wastes of a human population. Currently, the world human population has an ecological footprint that would require 1.5 Earths to supply the resources and assimilate the wastes of the current human population indefinitely. It is estimated that a sustainable level of ecological footprint would be 2.1 ha per person at our current population size, but that overall, the human population currently exceeds this by a wide margin. Obviously, this level of consumption and waste production is not sustainable. But examining this ecological footprint in more detail, we see that its size varies tremendously from country to country. The United States and certain European, Asian, and Middle Eastern countries have ecological footprints of 6 ha per person or higher, whereas countries such as India, Haiti, and many African countries have ecological footprints below 1 ha per person (Fig. 8.8).

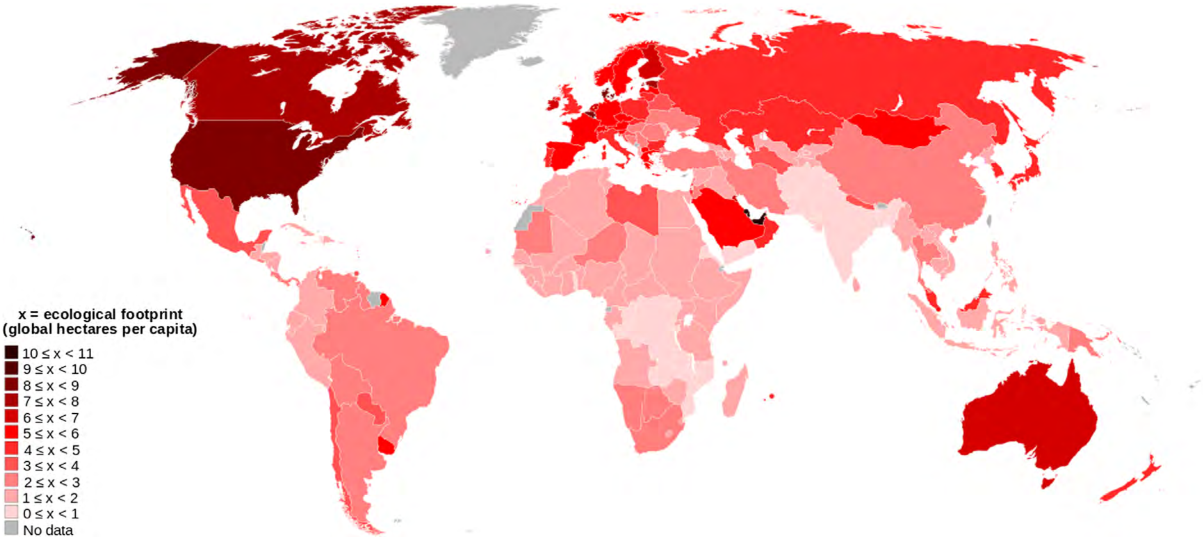


Figure 8.8: World map of countries, showing their per capita ecological footprint. (Wikipedia 'List of countries by ecological footprint;' Attribution: Jolly Janner)

Not surprisingly, there is a high correlation between ecological footprint and quality of life, and billions of people in poorer countries aspire to the lifestyle (and consumption levels) of the richest countries. While it may seem to be morally just, elevation of the entire world to the level of consumption of the richest countries would be ecologically disastrous. But it is possible to have a fairly high quality of life with a relatively low ecological footprint. Fig. 8.9 shows the ecological footprints and human development index values for countries in different regions of the world. The **human development index** combines three factors (life expectancy, educational level, and income) to derive a measure of quality of life. As the upper left region of the graph shows, some countries are succeeding in achieving a relatively high human development index while still maintaining a low ecological footprint. Cuba and several other Latin American/Caribbean countries fall into this category, as well as some countries in other regions of the world. However, other countries have similar quality of life (human development index), but with much higher environmental impacts (ecological footprint). These latter countries might benefit from an examination of what the countries with lower ecological impacts are doing right. In addition to population control, decreased consumption by the wealthier countries with large ecological footprints is essential to a sustainable global human population, but there are immense political obstacles to overcome in order to achieve this.

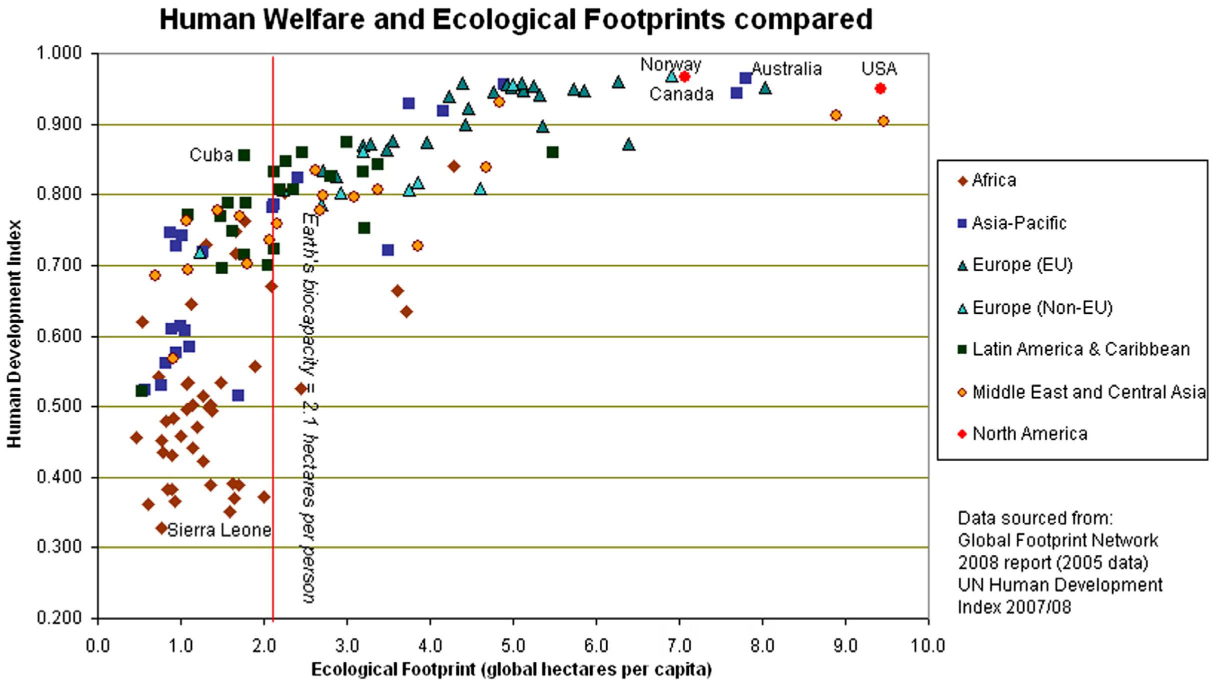


Figure 8.9: Ecological footprint for different nations compared to their human development index. (Wikipedia 'Ecological footprint;' Attribution: Travelplanner based on data from UN Development Programme and Global Footprint Network)

8.5 HUMAN IMPACTS ON OTHER SPECIES

As we have seen, humans and our activities have had immense impacts on the rest of the biological world. In geological history, there have been five extinction events that biologists consider "mass extinctions." The Permian-Triassic extinction event and the Cretaceous-Paleogene extinction event that included the non-avian dinosaurs are probably the two most well-known. The recent Holocene (or Anthropocene) has seen extinction levels that many biologists consider to be the 6th mass extinction. The Holocene extinction rate has been estimated at 140,000 species per year, with most of those being undocumented.

These extinctions include such recent and well known ones as the flightless dodo of the island of Mauritius, the thylacine of Tasmania, Australia, and New Guinea, and the passenger pigeon of North America. The dodo was driven to extinction in the late 17th century, apparently through a combination of habitat loss, mortality caused by introduced animals that plundered dodo nests, and human hunting. The thylacine (Fig. 8.10), also known as the Tasmanian wolf or Tasmanian tiger, was officially considered extinct in 1936, when the last captive specimen died at the Beaumaris Zoo in Hobart, Tasmania. The passenger pigeon was probably the most abundant bird in North America, with numbers estimated at up to 5 billion at the time of European arrival. The bird was driven to extinction by hunting and loss of habitat; the last individual died at the Cincinnati Zoo in 1914.

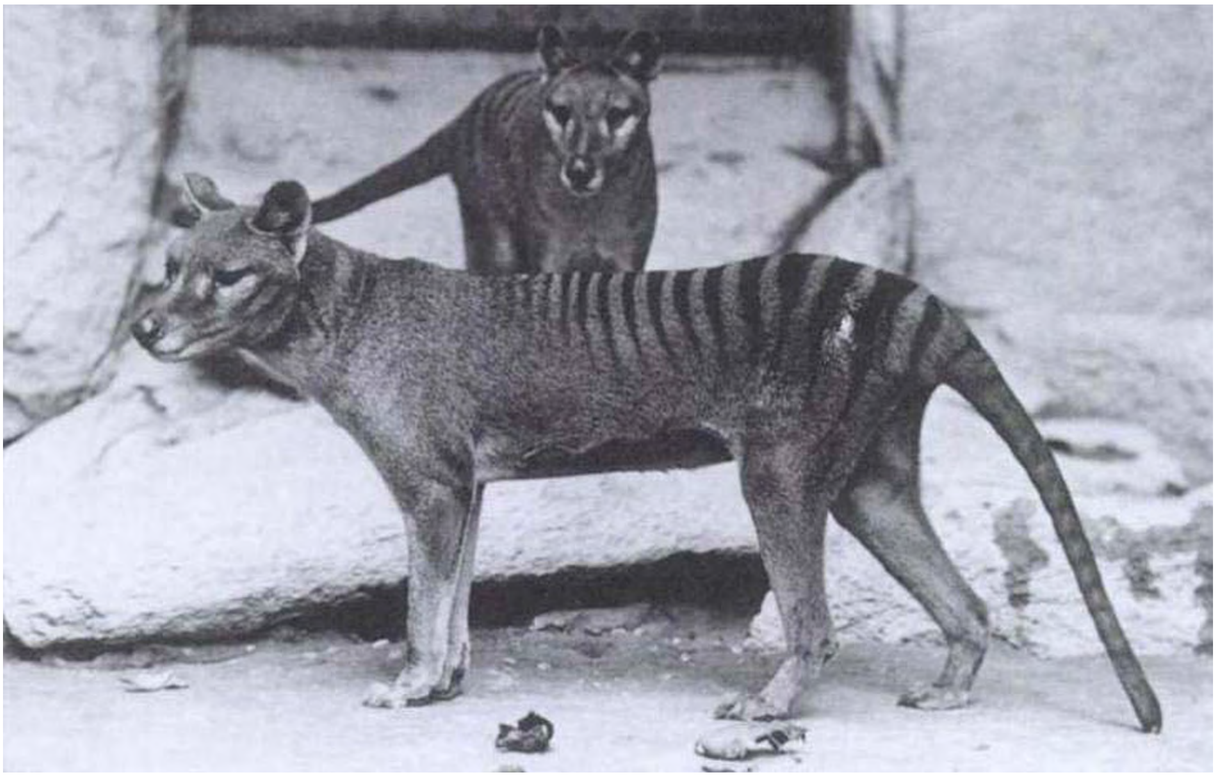


Figure 8.10: Thylacines in Washington DC, USA, 1906.
(Wikipedia 'Thylacine;' Attribution: Baker; E.J. Keller)

For every high-profile extinction such as these, countless species have disappeared before they were even known to science. For most of human history, our primitive hunting abilities and small numbers probably made the impacts of our hunting on other species negligible. But as we have seen, by the Pleistocene, human hunting capabilities had advanced to the point that it probably played a role in the Pleistocene megafaunal extinctions. Modern human hunting on an individual basis is regulated in many countries, and this can allow sustainable harvesting of wild game. However, on a large-scale, commercial level, human predation on other species of animals has reached a level that, according to a recent study by Chris Darimont and colleagues, now makes *H. sapiens* a "super predator," with the ability to cause mortality rates far in excess of those caused by non-human predators. For example, humans kill adult reproductive members of prey species at rates up to 14 times higher than do other predators; terrestrial carnivores and fishes are exploited especially intensely. This level of exploitation reflects both the hyper-efficiency of many human harvesting technologies as well as the demands of feeding the large and highly consumptive human population. Of course, these human hunting pressures affect not only the species being harvested, but other species in the food web that depend on them.

Since the beginnings of agriculture, *H. sapiens* have transformed the Earth's landscape. This transformation has undoubtedly been the most important source of anthropogenic extinctions. Over the last few centuries, this transformation has occurred in an accelerating fashion, due both to our increasing population and our increased technological abilities to alter the landscape. Columbus' 1492 voyage to the New World marked the beginning of a large-scale exchange of plants, animals, people, and technology between the Old and New Worlds, often referred to as the Columbian Exchange. One result of this exchange was the growth of Europe as an economic power; this would in time lead to colonialism and large-scale establishment of exploitative plantation economies in which primary products such as crops, timber, and extracted minerals would be produced using cheap (slave) labor in the colonies and then exported to the home country where the materials would be processed and re-exported at a large profit.

From a land-use standpoint in the colonies, this system would result in large areas of forest being cut and large areas of land being converted to agriculture with, of course, an accompanying loss of native biodiversity. Since then, of course, humankinds' ability to alter the landscape has dramatically increased in geographic scope and impact. In many parts of the world, such as the Midwestern U.S.A. where I live, one would be hard-pressed to find even a few hectares of contiguous land that does not show significant human impacts. This degradation and fragmentation of landscapes has resulted in small islands of suitable habitat in an ocean of agriculture and urbanization. As we saw in Chapter 6, smaller, more isolated oceanic islands have lower species richness; this pattern applies to terrestrial habitat islands as well.

As mentioned previously, the Columbian Exchange involved large-scale movement of species between the Old World and New World, so introductions of exotic species are not a new phenomenon. In many cases, these were economically important crops or domestic animals, and the ecological damage associated with them was to a large extent a function of land-use patterns in their new homes. The terms exotic and invasive are sometimes used interchangeably, but there is an important difference between the two. An **exotic** species, also known as an introduced, alien, or non-native species, is one that has arrived at a location outside its native geographic range, usually through human transport. Exotic species often, but not always, become invasive species. An **invasive** species is a (usually) exotic species that tends to proliferate and spread, causing ecological, economic, or even health-related harm.

Invasive species are often "*r*-strategists" rather than "*K*-strategists." In ecology, these two concepts relate to selection pressures for different life history traits. Species that are ***r*-strategists** can quickly colonize new locations. They tend to be relatively small-bodied and short-lived, but have rapid reproduction and growth. Offspring receive little or no parental care and have low survival rates, but because so many are produced, large enough numbers still survive. These species can disperse and spread rapidly. They are generally poor competitors, and depend on exploitation of newly-available environments with less crowded ecological niches to perpetuate themselves. Examples of *r*-strategists include ruderal or "weedy" plant species such as dandelions and many grasses, many insects and other invertebrates, and, among the mammals, many rodent species. ***K*-strategists** show the opposite traits (long-lived, slow reproduction but lots of parental care, good competitors, etc.), and include many tree species, orchids, and mammals such as primates and elephants. It is important to keep in mind that the *r*- vs. *K*-strategist concept represents a continuum, and that both types of traits can sometimes be found in the same species.

There are also other factors that can play a role in a species becoming invasive. If natural enemies or competitors kept the exotic species in check in its native environment, the absence of those species in the new environment can allow **ecological release** of the exotic species populations, resulting in an invasive species. Likewise, an exotic species can become invasive if an important limiting resource is more abundant in the new environment. There is also evidence that many invasive species are capable of undergoing rapid evolution, allowing them to quickly adapt to new environments. Islands and disturbed environments appear to be particularly susceptible to invasive species, probably because of lack of effective natural enemies and competitors, and greater availability of open ecological niches.

There is abundant evidence that invasive species can drive down numbers of other species and thus contribute to loss of biodiversity. On the western Pacific island of Guam, the brown tree snake was accidently introduced from the Indonesian region sometime in the late 1940s-early 1950s. Since then, this snake has created havoc, causing the extinction of 12 native bird species on Guam. Because of the greater abundance of food resources than in its native environment, brown tree snakes have reached densities of 100 individuals per ha on Guam. Plants can also be invasive exotics. Old man's beard is a climbing vine that was introduced as an ornamental plant in New Zealand in the early 1900s (Fig. 8.11). The seeds germinate most readily on disturbed ground. Once established, vines can cover trees and form a dense canopy that prevents sunlight from reaching the ground. This adversely affects native vegetation already present, as well as inhibiting germination of new individuals. In the Tierra del Fuego region of extreme southern Argentina and Chile, introduced beavers are radically changing the landscape and adversely affecting native species through their tree-felling and dam-building habits. These beavers are descendants of ones evidently imported from Canada by the Argentinian government in the 1940s in an attempt to establish a commercial fur trade. The beavers are now the focus of what may be the largest eradication project ever attempted, but it now appears that control, rather than eradication, is a more realistic goal.

Figure 8.11: Old man's beard (*Clematis vitalba*) smothering a New Zealand endemic, *Cordyline australis*, on the Port Hills in Christchurch. (Wikipedia 'Old man's beard in New Zealand;' Attribution: Alan Liefting)

8.6 ANTHROPOGENIC CLIMATE CHANGE

Like any other species, humans have always affected, and in turn been affected by, their environment. But with the dawn of agriculture, the ability of *H. sapiens* to alter the Earth increased dramatically, and reached even greater levels during the Industrial Revolution, which began in the mid- to late 1700s. Since that time, habitat destruction, invasive species introductions, and extinctions have continued and accelerated. But in the last few decades it has become increasingly apparent that industrialization is driving another and potentially greater threat to the Earth's biota – **anthropogenic climate change** or **global warming**. Certain gases in the Earth's atmosphere trap the sun's radiation, preventing it from being reradiated, a phenomenon known as the "greenhouse effect." It is this greenhouse effect that keeps the Earth's temperature high enough to support life. But since the Industrial Revolution, fossil fuel use has increased the amount of greenhouse gases, particularly CO_2, in the atmosphere. Evidence has increasingly pointed to this rise in greenhouse gas emissions (Fig. 8.12) as a major factor in global climate change and an overall warming trend that has the potential to cause catastrophic disruption of the Earth's biosphere.

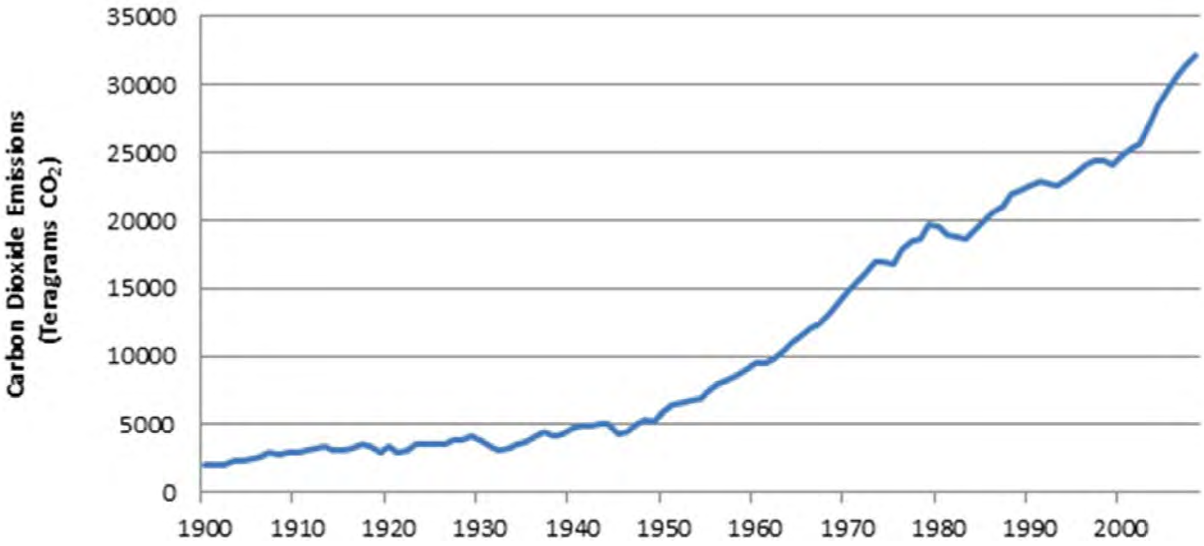


Figure 8.12: Fossil fuel related carbon dioxide (CO_2) emissions over the 20th century. (Wikipedia 'Global warming;' Attribution: U.S. Environmental Protection Agency)

Studies of the potential effects of increased atmospheric CO_2 go back over a century. In 1896, Swedish physical chemist Svante Arrhenius suggested, and attempted to calculate, how changes in atmospheric CO_2 levels could affect temperatures at the Earth's surface via the greenhouse effect. While the details of his predictions were inaccurate, Arrhenius was one of the earliest scientists to show that the possibility of anthropogenic global warming should be taken seriously.

Debate among climate scientists regarding the potential role of atmospheric gases in climatic change continued throughout the 20th century. By the early 1970s, it was apparent that aerosols were increasing in the atmosphere, but there was disagreement regarding whether these increased aerosols would likely result in global warming or cooling. Although the scientists who predicted cooling were a small minority, their views were exaggerated by the mainstream media. By the 1980s, it was becoming increasingly clear that any cooling effect that might result from atmospheric aerosols would be negligible compared to the heating of the Earth's climate due to atmospheric CO_2 levels. Climate models indicated a positive relationship between atmospheric CO_2 and global temperatures. In 1985, a Franco-Soviet study of Antarctic ice cores, led by Claude Lorius, showed that past temperatures and CO_2 levels had tracked each other closely, providing important evidence for a CO_2-temperature relationship independent of computer climate models.

In 1988, the United Nations established the Intergovernmental Panel on Climate Change (IPCC). The IPCC periodically issues reports on the state of scientific knowledge regarding climate change. The first report was issued in 1990, with subsequent reports every 5 to 7 years. The fifth and most recent IPCC assessment report was issued in 2014. The reports have reflected increasing concern and certainty among climate scientists regarding climate change and humanity's role in causing it. The fifth report states that the influence of humans on the Earth's climate is clear, with a very high (≥ 95%) probability that human influence was the dominant cause of the dramatic global warming trend between 1951 and 2010 (Fig. 8.13). Furthermore, without new policies to address climate change, the report projects an increase in global mean temperature of 3.7 to 4.8°C by the year 2100, relative to pre-industrial levels. It appears unlikely that some level of global warming can be avoided at this point. The fifth IPCC report indicates that if pledges made at the 2010 United Nations Climate Change Conference are met, then there is likely a chance of limiting this temperature increase to below 3.0°C by 2100.

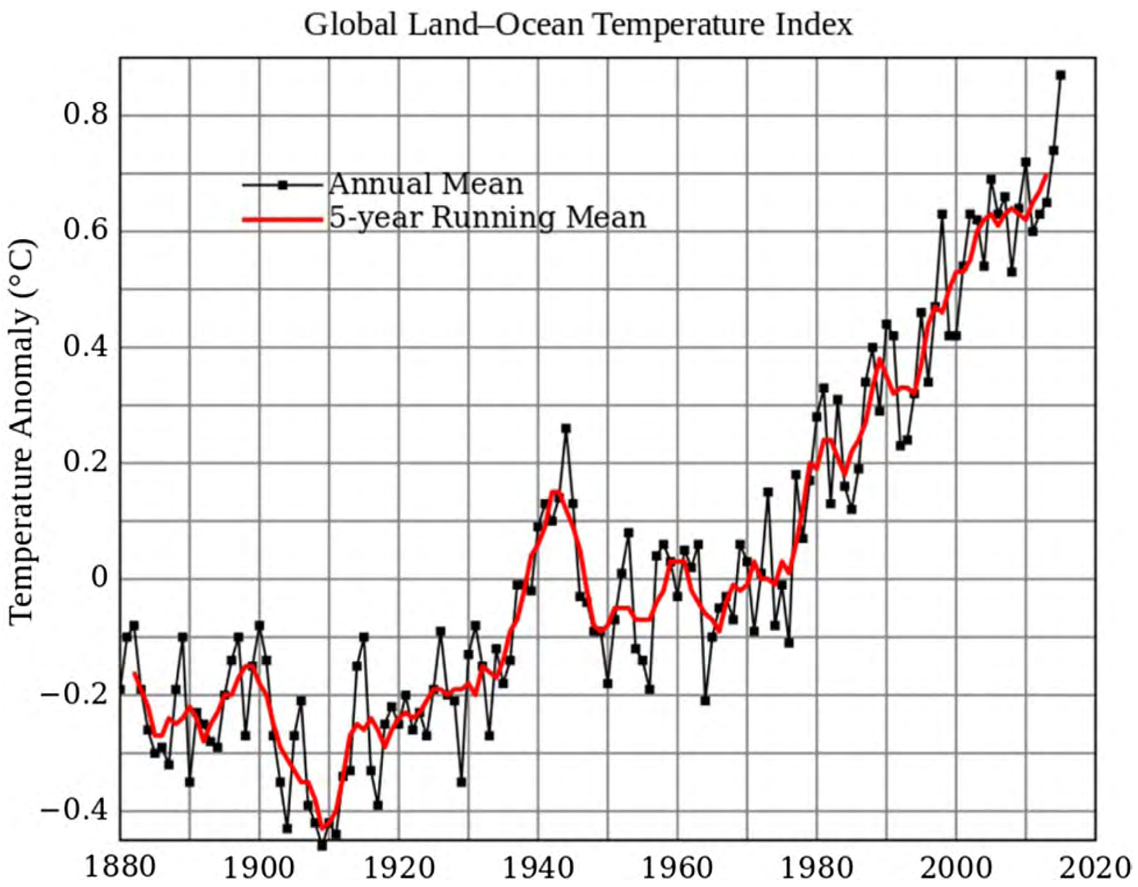


Figure 8.13: Global mean surface temperature change from 1880 to 2015, relative to the 1951–1980 mean. The black line is the annual mean and the red line is the 5-year running mean. (Wikipedia 'Global warming;' Attribution: U.S. National Aeronautics and Space Administration)

These changes in climate will have a variety of impacts on the Earth's biota. At the biome level, ecologist Wilfried Thuiller has calculated that, for each 1°C change in global temperature, the world's biomes will shift about 160 km in latitude. So, for the above predicted temperature changes, the world's biomes would shift roughly 500 km to 750 km northward, assuming other factors such as soil type are not limiting. Of course, individual species will vary in their responses to climate change, depending on their physiological tolerances and the responses of other organisms on which they depend. An example of the latter has been documented by Nicole Miller-Struttmann and colleagues for alpine bumble bees on three peaks in the Rocky Mountains of Colorado, USA. Bumble bee species and communities there have undergone decreases in tongue length over the past few decades, probably as a result of decreases in the availability of floral resources due to the warmer summers. Specialist long-tongue bees have declined at the expense of the favored generalist short-tongue bees, and this has led to a mismatch between the shorter-tongued bees and the longer-tubed plants that they once pollinated. The differential response of species to climate change could result in the severing of ecological linkages such as pollination, seed dispersal, and parasitism.

Climate change will likely have dramatic impacts on the biogeography of infectious diseases as well. Higher temperatures and associated extreme weather events will cause greater flooding and increased habitat for disease vectors such as mosquitoes that breed in aquatic habitats. Higher temperatures will also mean faster developmental rates of these insects, as well as increased geographic and altitudinal ranges in some species. This means that mosquito-borne diseases such as malaria and dengue virus that have been considered primarily tropical diseases could become established in areas where they previously have not occurred or have been eradicated. This is a particularly dangerous situation because most people in these locations would have low levels of immunity and little experience with the diseases. The abundance and distributions of other important disease vectors such as ticks, black flies, and lice will probably be affected as well, in some cases unpredictably. Climate change could also increase the impacts of infectious diseases indirectly if extreme weather events and disruptions of agricultural systems cause food shortages, since malnourished individuals are more susceptible to the effects of disease.

As human activities change the Earth's landscape and ecological systems, biogeographers will be called upon to predict the likely impacts of these changes on the planet's biota, and to provide expert guidance in mitigating the adverse effects of these impacts. The science of biogeography promises to be at the forefront as humanity and the living things with which we share the planet face a challenging future.

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