PART

SPACE AND LIFE
Biogeography is a very broad science, and biogeographers are a highly diverse group of scientists. This multidisciplinary scope is one of the most satisfying aspects of biogeography—and one of the most challenging. Biology, geography, and geology all contribute concepts, specialized vocabularies, and ways of classifying information that are important to biogeography. In order to understand and appreciate the science of biogeography, we must therefore have some knowledge of its foundations in these other sciences. Before we get down to the business of biogeography, we will review some key concepts from these associated disciplines. In this chapter, we will concentrate on aspects of biology and physical geography that are fundamental to biogeography. Later in this book we will discuss some concepts from geology that are also important to biogeography. Much of the material that we cover here will be familiar to anyone who has taken introductory courses in biology and physical geography. However, even for those with such a background, a little review won’t hurt.

**BIOLOGY AND THE HIERARCHIES OF LIFE**

Biology can be defined as the science of life and all of its phenomena. Life on earth includes millions of different types of organisms, ranging from viruses to whales. The study of any of these organisms could include examination of myriad phenomena, from biochemical reactions to social behavior. It is clear that biologists face a daunting challenge! The science of biology tackles this immense task by breaking it down into smaller components that can be studied individually. One way to categorize and organize the constituent units of a large entity is to develop a hierarchy. A hierarchy is a system of organization in which components are ordered by rank. Most corporations are good examples of hierarchies. A large group of office staff is under the direction of one office manager, who, along with several other managers, is under the direction of the vice president of operations. The vice president, along with two or three other vice presidents, reports to the president of the firm. The president is at the top of the hierarchy, and the office staff is its base. Every biogeographer should be familiar with three important biological hierarchies: the taxonomic hierarchy, the ecological hierarchy, and the trophic hierarchy. We will examine each of these.

**Taxonomic Hierarchy**

**Taxonomy** is the subdiscipline of biology concerned with the classification and naming of organisms. Taxonomy is also known as **systematics** when the main goal is to determine the evolutionary relationship between groups of organisms. In this case, taxonomists are also called systematisists. The evolutionary histories of
organisms that are reconstructed by systematists are referred to as phylogenies. Taxonomists use observable traits, referred to as characters or character states, to group similar individual organisms together and to separate groups of different organisms. The groups that taxonomists develop are called taxa (the singular form is taxon). The characters that taxonomists use to classify organisms usually start with physical differences, such as color variations in flowers or in the plumage of different birds. Taxonomists may also consider differences that are apparent through chemical analysis of the tissue or fluids of the organism. Such studies are referred to as chemotaxonomy. Finally, cytotaxonomists examine the chromosome structure of organisms to detect genetic similarities and differences in order to classify organisms.

The classification and naming of organisms by individual taxonomists would not be very useful if everyone had their own system and terminology. Fortunately, there is a single system of taxonomic classification that is generally accepted by all biologists and biogeographers. The development of our present taxonomic system is at the foundation of biology and biogeography. It is a history that can be traced back to ancient Greece. The roots of the modern taxonomic system began with Aristotle (384–322 B.C.). Aristotle, a student of Plato, is best known as a philosopher but was also active in biology, physics, astronomy, and psychology. He developed an early scientific system for classifying animals into groups that shared similar features. Aristotle believed that the specific form and behavior of individual plants and animals were inherited and immutable. He considered that all individuals belonged to groups, or species (from the Greek word “eidos”), of taxonomically similar individuals. Aristotle believed that the form and behavior of these species did not change from generation to generation. He taught that dogs form one species and cats another. Aristotle also argued that plant and animal species formed a hierarchy ranging from simple organisms, such as worms, to the most complex organism, which he considered to be humans. In the Middle Ages, European scientists, influenced by Aristotelian logic, grouped organisms that appeared to be generally, but not exactly, similar to each other into taxonomic units called genera (the singular form is genus). A genus would include, for example, the Scots pine trees of Scandinavia and the Mediterranean pines of southern Europe. Both the Scots pines and the Mediterranean pines belong to the genus called Pinus.

Before we proceed, let’s examine the words “genus” and “species” and consider the continuing role of Latin in biology and biogeography. Genus is the Latinized form of the Greek word “genos.” In the Middle Ages the language of scholarship in Europe was Latin, and the names of the genera came from that language or are latinized versions of words from other languages. For example, in Latin the genus for pines is called Pinus. In comparison, the genus for cats is Felis. Although Latin is no longer widely spoken or understood, the formal names of organisms are still written in that language. The benefit of this convention is that no matter which language the scientist is working in, the names of the organisms are always presented in Latin using the Latin alphabet. Even papers and books written in Russian Cyrillic or Chinese characters will always present the scientific names of organisms in the Latin alphabet. Biologists and biogeographers always know which organisms are being discussed, even if they can read nothing else in the document. The use of the proper scientific names for organisms is also important for avoiding confusion among scientists who speak the same language. Take pines, for example. In North America we have many different trees that are
closely related and belong to the genus *Pinus*. In the South Pacific, you might encounter a tree that is commonly called the Norfolk Island pine. This plant, however, is unrelated to our North American pines and belongs instead to the genus *Araucaria* (Fig. 2.1). In many instances the same plant or animal will have several different common names, but every organism has only one accepted scientific name. In addition, the Latin names of organisms often contain descriptions that can be understood by people with only a limited knowledge of Latin.

So, what is the difference between a species and a genus? It is recognized that genera of plants and animals contain organisms that are related but are consistently distinguishable on the basis of their morphology. In addition, many of these taxa, though members of the same genus, cannot interbreed. These different members of a genus are species. For example, people in eastern North America will be familiar with the eastern white pine, and those in the western part of the continent might know the lodgepole pine. Both species belong to the genus *Pinus* and share certain broad similarities, such as possessing long thin needles, cones, and upright growth (Fig. 2.2). There are, however, clear differences between the trees. White pines can grow to well over 30 m in height, whereas most lodgepole pines only achieve heights of 20 m. The white pine carries its needles in bundles of five. In contrast, the lodgepole pine has bundles of two needles. The white pine has large cones that open immediately upon ripening and release...
their seeds. Lodgepole pines have small cones, many of which remain closed and retain their seeds until a fire causes the cone scales to open. In addition, eastern white pine and lodgepole pine cannot interbreed. The two trees are recognized as different species within the genus *Pinus*. Following the concepts of Aristotle, the English scholar John Ray (1627–1705) attempted to systematically define a species. He concluded that if seeds came from the same plant, the seedlings must be related and similar in character. He recognized that variations might occur between seedlings from the same parent, but he considered these to be “accidents.” Ray’s conception of species can be paraphrased as “Like begets like.”

Since the time of Ray, species have formed the basic unit of the modern taxonomic system, but there remains much debate among scientists as to just how a species should be defined. Three main definitions are in use today. The *phylogenetic species concept* identifies a species as a group of sexually reproducing organisms that share at least one diagnostic character that is present in all members of the species but absent in other organisms. Unique behavioral traits are accepted as defining characters. This concept does not adequately take into account natural variations within species, such as differences in human hair color. If this concept were widely applied by biologists, far more species would be identified than is now the case. In addition, the phylogenetic species concept does not consider reproductive interactions between members of the species or their evolutionary history. The *biological species concept* defines a species as a group of organisms that can interbreed freely under natural conditions. This definition was articulated by the great evolutionary biologist Ernst Mayr in 1942, although its roots extend into the early part of the twentieth century. It remains the most widely used definition of a species in biology. Finally, paleontologists who study the fossil record often use the *evolutionary species concept*. Evolutionary species are organisms that have a direct ancestor-descendant relationship that is traceable in the fossil record. Usually, such a relationship is inferred from morphological similarities such as the size or shape of the fossils. This is because morphological features are generally all that is available from the fossil record. New species are differentiated when there are clear divisions of one evolutionary line into two or
more new lineages. The evolutionary species concept allows for morphological changes in the species over time as evolution occurs.

In practice, biogeographers combine these concepts and view species as organisms that are morphologically similar and can interbreed freely under natural conditions. It is assumed that such organisms must share a common ancestor. Although this sounds pretty straightforward, we still encounter problems in defining species due to natural variability in the morphology and reproductive behavior. In addition, species are generally thought of in terms of sexually reproducing organisms. Organisms that reproduce asexually raise difficulties when the common phylogenetic and biological species definitions are used.

Until the eighteenth century, scientists named species simply by adding some descriptive words to the name of the genus. The eighteenth century was a period of great geographical and biological exploration and discovery when many new genera and species were found and described. To differentiate these newly discovered species, their names often became polynomials containing a dozen or more Latin words. Clearly, this system was unwieldy. The simplified system of naming organisms that we use today was invented in the mid-eighteenth century by the great Swedish scientist Carolus Linnaeus (1707–1778). He attempted to catalog all of the known species of the world. Linnaeus was trained as a medical doctor but inherited a keen interest in plants and natural history from his father. Many of the species he identified and described are still accepted by taxonomists today. Linnaeus introduced the binomial system whereby every organism could be identified by a unique combination of a generic (genus) and specific (species) name. For example, white pine is known as Pinus strobus, while lodgepole pine is known as Pinus contorta. These related species share the same genus, Pinus, but are differentiated by their species names, strobus and contorta. Species with the same generic names are assumed to be related. With the binomial system, different species can also share the same specific name. This occurs frequently because the specific names often describe some feature of the organism and in no way implies a genetic relationship.

Because different, unrelated species can share the same specific name, a species is never referred to by its specific name alone—the genus must be indicated. If it is clear which genus is being discussed, you can use the first initial of the generic name instead of spelling the complete name (i.e., Quercus alba can be referred to as Q. alba). By convention, the generic and specific names are always italicized, and the generic name starts with a capital letter. The specific name starts with a lower-case letter. In this book you will find the scientific names of important genera and species in parentheses following the first usage of the common name. Sometimes the scientific name of a species is followed by the full name, abbreviated name, or initials of the taxonomist who first described it. A scientific name followed by the letter L, such as Quercus alba L., means that the species was first described by Linnaeus himself.

So what does the modern taxonomic hierarchy consist of? As we have seen, species form the lowest level of the hierarchy, although some species may be further subdivided into distinctive subspecies and races. Collections of species that are similar to one another, and presumably related, are grouped together in the next level, the genera. Genera that are morphologically similar and likely possess evolutionary linkages are grouped together as families. Oaks, for example,
belong to the family of trees called Fagaceae. This family also includes the genus beech (Fagus) and several other genera of trees. How families and higher taxonomic groups are classified remains a subject of revision and debate. According to one classic system, families that are related are grouped together in taxonomic orders. The order for oaks is Fagales. In turn, orders are grouped into classes. All flowering plants (sometimes called angiosperms or the Magnoliophyta) are grouped into one of two classes. The oaks are placed in the class Dicotyledons (also called Magnoliopsida). Among other traits, plants in this class have seeds that produce two initial leaves, or cotyledons, when they germinate. Many of the familiar trees of the deciduous forest, such as maples (Acer), birch (Betula), elm (Ulmus), willows (Salix), and garden flowers such as roses (Rosa) and daisies (Aster) are dicotyledons. The other class for flowering plants is Monocotyledons (also called Liliopsida). Some examples of monocotyledons include orchids (Orchidaceae) and grasses (Poaceae). When the seeds of these plants germinate, they produce one cotyledon.

Classes are grouped together into phyla (the singular is phylum). The phylum for the dicotyledons and monocotyledons is Anthophyta. The Anthophyta are also referred to as the flowering plants. Conifers (cone-bearing plants) such as the pines, the spruces (Picea), and the firs (Abies) are neither dicotyledons nor monocotyledons. They do not belong to the Anthophyta but are instead members of the phylum Coniferophyta and are also known as gymnosperms. Finally, at the highest level, the phyla are grouped into five kingdoms or sometimes a lesser number of domains. Debate continues on how to classify organisms at many levels, including at this highest level. According to one system, the Kingdoms include Monera, Protista, Fungi, Plantae, and Animalia. The Monera are simple prokaryotic organisms such as bacteria. The Protista are single-celled eukaryotic organisms such as amoeba. You can probably guess who the members are of the Fungi, Plantae, and Animalia kingdoms. Thus, we can trace the affinity of every organism, including humans (Table 2.1), up through the taxonomic hierarchy to a kingdom. However, the exact number of kingdoms continues to be debated.

The taxonomic hierarchy provides a convenient and accepted way to classify life. It should be remembered, however, that this system is not static. New species are continuously being discovered and added. At times, new genera and families are added. Even the status of different kingdoms is debated. In addition, taxonomists may change the genus or family of older recognized species when new information comes to light. It sometimes happens that several taxonomists

<table>
<thead>
<tr>
<th>TABLE 2.1 A Systematics (Taxonomic Hierarchy) of Eastern White Pine (Pinus strobus) and Humans (Homo sapiens sapiens)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>White Pines</strong></td>
</tr>
<tr>
<td>Species</td>
</tr>
<tr>
<td>Genus</td>
</tr>
<tr>
<td>Family</td>
</tr>
<tr>
<td>Order</td>
</tr>
<tr>
<td>Class</td>
</tr>
<tr>
<td>Phylum</td>
</tr>
<tr>
<td>Kingdom</td>
</tr>
</tbody>
</table>
identify the same species and give it different names. These names are referred to as synonyms, and the earliest published name generally takes precedence.

**Ecological Hierarchy**

The taxonomic hierarchy provides for a division and ranking of life based on the morphology and the evolutionary relationship of organisms. It is the foundation for many aspects of biological research. It does not, however, provide much guidance for the ecologist or biogeographer who goes out into the field to study how organisms are affected by the environment or how they interact with other species. It would be an intractable task to set out to study the relationship between every organism with the environment and all other organisms. Therefore, ecologists and biogeographers often concentrate on specific spatial and taxonomic scales of study. These levels of ecological study can be organized into a hierarchy that reflects the increasing geographic and taxonomic scale being examined.

The lowest scale of study that is of interest to the biogeographer is the individual organism. For example, scientists might put a radio tracking collar on one arctic fox (*Alopex lagopus*) and monitor its movements. At the next level, they might consider studying a **population** of arctic foxes. A population is defined as all individuals of a given species in a prescribed area. Usually, members of the same population are assumed to be in close enough proximity to be able to interact and interbreed frequently. Of course, in many cases, members of the same species are found in different locations and do not interact on a regular basis. Interbreeding and other interactions between these separated populations of the same species may only occur relatively frequently or extremely infrequently. Such populations are referred to as **metapopulations**. Two broad types of metapopulations can be recognized. **Loose metapopulations** consist of subpopulations of the same species that live in different locations and interact with other subpopulations very infrequently. The distance between subpopulations is farther than most individuals travel during their life spans. **Tight metapopulations** consist of subpopulations that are close enough for individuals to travel between them and thus interact more frequently. The arctic fox populations living on different islands in the Canadian arctic separated by large expanses of water are an example of a loose metapopulation. Birds that live and nest in different woodlots that are separated only by agricultural fields are an example of a tight metapopulation.

We might also consider examining the interaction of our fox population with all the other species of organisms in its environment. In this case, we are studying an ecological **community**. A community can be broadly defined as all populations of organisms that live and interact within a prescribed area. Ecological research that focuses on one species is sometimes referred to as **autecology**, while research that focuses on the interactions between species in communities is referred to as **syneccology**. Some ecologists and biogeographers limit their studies of communities to subsets of the total community. For example, phytogeographers might restrict their study to flowering plant species only. Some biogeographers would refer to this as the flowering plant community. However, other ecologists and biogeographers feel that the term community should only be used to refer to all species of organisms in an ecosystem. Subsets of a community, such as the flowering plant species, are often referred to as **assemblages**. One important subset of the complete community is the guild. **Guilds** are groups of animal species within a community that have similar forms, habitat, and resource requirements. The insectivorous bird species form one guild in a community, while the seed-eating bird species form another.
If we were to consider the relationship between the species of our community and the physical factors of the environment, particularly when we examine flows of energy and matter through this biophysical system, we would be conducting research at the scale of the ecosystem. It could be argued that the spatial boundaries of any ecosystem extend over the whole earth. Even the smallest area is linked to the world at large by physical processes such as rainfall and biological processes such as the input of fine airborne organisms. In practice, the boundaries of ecosystems are often defined by the researcher and can vary from very small areas such as the trunk of a decaying tree to large areas such as the tundra of Baffin Island in arctic Canada. Very large areas of the earth’s surface that have a similar climate and vegetation are referred to as biomes. The biomes are an important area of research in biogeography, and we will discuss them in detail later. Finally, all of life on the planet is collectively referred to as the biosphere—the highest and broadest level of ecological research. The other realms of the earth are physical ones of the atmosphere, hydrosphere, and lithosphere. The atmosphere includes all the components of the air; the hydrosphere includes all the water in the oceans, lakes, streams, and ground; and the lithosphere is the solid earth of rock and sediment. Although the research of biogeographers may focus on smaller levels such as ecosystems, the end goal of biogeography is to combine the results from all of these more specific studies and draw general conclusions about how the biosphere functions today, how it developed, and where it might be headed in the future. Remember, our future and that of the biosphere are really one and the same.

**Trophic Hierarchy**

A third way of ordering the biosphere is to examine the flow of energy through ecosystems. The various levels through which energy flows from its initial capture by the biosphere until its dissipation as waste heat are called trophic levels. The biosphere functions through the acquisition of energy by organisms and the flow of energy from one organism to another. With very few exceptions, all life is dependent on the sun to provide the energy that is consumed. Notable exceptions are the amazing ecosystems that have developed around undersea volcanic vents (Technical Box 2.1).

Most of the solar energy that reaches the earth is visible light, which is a form of short-wave radiation. The electromagnetic waves that make up visible light range in wavelength from ~0.4 to 0.6 microns. Of this incoming energy, approximately 32% is reflected back into space by the earth’s atmosphere. Roughly 18% is absorbed by the earth’s atmosphere. The surface of the earth absorbs about 50% of the incoming radiation, and about 20% of this is used in evaporation. Visible light energy from the sun is absorbed by the atmosphere and the earth’s surface and then radiated as long-wave (3–25 micron wavelength) thermal energy. This long-wave radiation is what we sense as heat. It is clear that almost 100% of the incoming solar radiation is reflected back into space or used in heating and evaporation. What then powers the biosphere? The entire biosphere, including the human race, is supported by a tiny fraction of the incoming solar radiation. The amount of solar energy captured for direct use by the biosphere is only 0.1–0.3% of the total input!

The solar energy used to power the biosphere is captured through the process of photosynthesis. For most plants, the radiation used for photosynthesis
Chemosynthesis and the Ecosystems of Oceanic Hydrothermal Vents

In 1977 scientists discovered that hydrothermal vents located 2500 m below the ocean surface near the Galapagos Islands supported unexpectedly dense concentrations of organisms. Similar vents have been discovered in both the Pacific and Atlantic oceans. The biomass of these vents is astounding and can range as high as 20–30 kg/m². The vent organisms include giant red worms (*Riftia pachyptila*), large clams (*Calyptogena magnifica*), and mussels (*Bathymodiolus thermophilus*). In addition, various species of crabs, shrimps, and sea anemones are found at some vents. In all, some 300 new species of animals have been discovered near undersea vents. How can such fauna be supported so far from the upper ocean waters where photosynthesis occurs? These vents emit mineral-laden waters at temperatures ranging up to 450°C. When mixed with the cold ocean waters, this produces temperatures in the vent area of 8° to 23°C. Hydrogen sulfide (H₂S) is particularly abundant in these plumes. Studies have revealed that these vents support a food chain based entirely on geothermal energy. At the base of the food chain are bacteria that oxidize the sulfur from the vents to form carbohydrates. In contrast to photosynthesis, this process is called **chemosynthesis** and proceeds as follows:

\[
\text{CO}_2 + \text{H}_2\text{S} + \text{O}_2 + \text{H}_2\text{O} \rightarrow \text{CH}_2\text{O} + \text{H}_2\text{SO}_4
\]

The CO₂ and O₂ in the process comes from the sea water. The bacteria are then eaten by primary consumers such as limpets, mussels, and clams. It is suspected that some other types of bacteria may utilize methane or ammonia from the vents in energy synthesis.
falls in the red through blue visible light (~0.4–0.6 micron wavelength) portion of the electromagnetic spectrum. This light is referred to as photosynthetically active radiation, or PhAR. Most of the solar energy that the earth receives is PhAR, so it is no coincidence that plants evolved to use this portion of the electromagnetic spectrum in photosynthesis. It is also not surprising that our eyes are adapted to detecting radiation in these wavelengths. We can see visible light spectrum energy but not ultraviolet or infrared energy.

During photosynthesis, atmospheric carbon and water vapor are transformed into sugar, water, and oxygen. The energy for photosynthesis comes from PhAR. The process takes place in chloroplasts, which are small, green bodies within plant cells. The chloroplasts hold chlorophyll, which is the primary light capturing the pigment of plants. The overall process can be summarized as:

\[
\text{Light} \quad 6\text{CO}_2 + 12\text{H}_2\text{O} \rightarrow C_6\text{H}_{12}\text{O}_6 + 6\text{H}_2\text{O} + 6\text{O}_2
\]

The CO₂ enters the leaves of plants through openings created by specialized sets of cells called stomata. The stomata also allow the release of oxygen and water vapor from the interior of the leaf.

There are three different biochemical pathways that green plants use in photosynthesis. Most plants capture energy using the C₃ pathway described by Melvin Calvin of the University of California at Berkeley. In C₃ plants, the CO₂ from the atmosphere is converted into a 3-carbon molecule called 3-phosphoglyceric acid. In the 1960s it was discovered that sugar cane converts CO₂ into two 4-carbon molecules: malic and aspartic acid. This process became known as the C₄ pathway. Finally, some plants, such as the prickly pear cactus (Opuntia), use a modified form of photosynthesis called crassulacean acid metabolism (CAM). In CAM plants, CO₂ is absorbed at night and stored as malic acid. During the light of day, photosynthesis is conducted by the C₃ pathway. In general, C₄ plants have the highest rates of photosynthesis, while CAM plants display the lowest rates. Interestingly, however, all plants are relatively inefficient in terms of energy fixation through photosynthesis. Only about 1% to 3% of the light hitting a leaf is transformed into chemical energy in the form of simple carbohydrates such as the sugars glucose and fructose.

Photosynthetic plants are the foundation of the trophic hierarchy (Figure 2.3). Plants are referred to as primary producers because they fix the energy of the sun into chemical energy used to power the biosphere. This term is slightly misleading, for plants cannot actually produce energy but merely transform it from one state to another. Plants are also referred to as autotrophs or phototrophs because of their ability to fix energy through photosynthesis rather than derive it from the consumption of other organisms. Organisms that eat plants to obtain energy are called primary consumers. Species that eat the primary consumers are referred to as secondary consumers, while species that eat secondary consumers are referred to as tertiary consumers. Plant-eating species are also called herbivores, and meat-eating species are called carnivores. Animals that eat both meat and vegetable matter, such as most humans, are omnivores. When plants and animals die, decomposers consume them. Decomposition is the ultimate fate of all trophic levels. Herbivores, carnivores, omnivores, and decomposers are collectively known as heterotrophs because they rely on other organisms to provide energy.
The trophic levels extending from primary producers to the highest level of consumers are sometimes called food chains. However, the idea that energy flows in a linear fashion up the trophic hierarchy is simplistic and misleading. Generally, there is a skipping of levels and a back and forth exchange between different levels of consumers and decomposers. As a result, the actual flow of energy in an ecosystem is more like a food web than a linear chain (Fig. 2.3). Elton (1927) was one of the earliest scientists to identify the importance of ordering ecosystems according to energy flows. He also recognized that the flow of energy was more complex than a simple linear chain. The work of Lindeman in 1942 was the first attempt to formally conceptualize and quantify the flow of energy within food webs. The study of food webs is the basis of modern systems ecology. It has been
suggested that understanding food web structure is fundamental to understanding basic ecosystem structure, function, and response to disturbance and change.

Relatively complex trophic hierarchies have been identified from both terrestrial and marine ecosystems. However, tracking and quantifying the flow of energy in such systems are not easy. The three approaches commonly used to investigate and define food webs are direct observation of feeding habits, inspection of the stomach contents of dissected organisms, and use of radioactive tracers such as phosphorus-32 (32P), which are introduced through injection into the vegetation and can be easily traced in tissue samples from animals.

The average length of time during which energy captured through photosynthesis is held by living plants in food webs varies from a few days in the open ocean to 3 years in grasslands and 22 to 25 years in some forests. Energy captured by photosynthesis can also be held in plant litter for significant periods of time before being used by decomposers. In the tropics, the energy held in plant litter may be released within three months, while it can be held for over 100 years in the litter of temperate and northern forests. However, studies using radioactive tracers show that, despite the potential long residence time of energy in plants and litter, much of the energy captured by photosynthesis moves very quickly through the food web. In both terrestrial and freshwater ecosystems, some of the energy captured by photosynthesis is passed up to the highest trophic levels within a matter of weeks.

Elton noted that trophic hierarchies appeared to be limited to only four or five levels. More recent examinations of the number of trophic levels in many food webs ranging from invertebrate communities living in dung to birds in forest stands to fish, birds, and mammals of the Antarctic pack-ice have found that most ecosystems support only three to six trophic levels. Why is this? It has been argued that since the transfer of energy between different trophic levels is relatively inefficient, the energy available to higher trophic levels will rapidly decrease. All organisms use energy to function through the process of respiration, which is the oxidative reaction that breaks the high-energy bounds of carbohydrates to release energy for the organism’s metabolism. Thus, respiration is the reverse of the process of photosynthesis, with metabolic energy being produced.

\[
\text{Energy + } 6\text{CO}_2 + 12\text{H}_2\text{O} \rightarrow C_6\text{H}_{12}\text{O}_6 + 6\text{H}_2\text{O} + 6\text{O}_2
\]

On average, only about 10% of the energy of any trophic level is passed on to the next trophic level. This generalization is known as the 10% rule. As a result of the 10% rule, each trophic level is expected to have about 90% less energy available to support it than the preceding trophic level. There is a high degree of variation in the actual energy efficiencies of different organisms in food webs. Birds and mammals are the least efficient because they use energy to maintain constant body heat. They assimilate only about 3% of the energy they receive in food. Insects have an energy efficiency of around 39%, while fish have efficiencies of around 10%. The decrease in available energy with each trophic level is extremely important in ordering ecosystems. When you consider how little energy is passed up through each trophic level, it is easy to understand why the bulk of all living things on earth are plants (perhaps >90% by mass) and very
large carnivores are rare, occurring at much lower numbers than their prey species. In theory, it takes a minimum average of 10 prey organisms to support one bird or mammal predator of equal mass.

The total number of consumers that any ecosystem can support is limited by the productivity of the plants. The productivity of vegetation is therefore a key focus of study for understanding the structure of ecosystems. The productivity of vegetation in fixing energy is known as primary productivity. Primary productivity can be viewed in two different ways. Gross primary productivity is the total energy fixed in an ecosystem by photosynthesis. However, since some of this energy is used through respiration to support the metabolic activities of the plants, not all of the photosynthetic energy is available to produce plant matter and be passed onto higher trophic levels. The gross primary productivity minus the energy lost by respiration is referred to as net primary productivity. So, how is net primary productivity measured? Many different techniques may be used, ranging from the measurement of carbon fixation and respiration losses of individual plants to satellite-based estimates of the photosynthetic activity of the world’s oceans. A relatively direct way is to harvest and weigh a representative sample of the plant matter produced during a given time period in a given area. In terrestrial environments, the plants can be harvested from both above and below the ground to produce an estimate of aerial and root production. The plant material is dried and weighed. The mass of living material is referred to as biomass. The plant biomass is used to calculate primary productivity as follows:

\[ dB = B_1 - B_2 \]

where

\[ dB = \text{the change in biomass between time period 1} \ (t_1) \text{ and time period 2} \ (t_2) \]

\[ B_1 = \text{biomass at time} \ t_1 \]

\[ B_2 = \text{biomass at time} \ t_2 \]

However, we must also account for losses in biomass due to death and decay of plants (L) and losses to consumers (G), so that the true net primary productivity = \( dB + L + G \). Net primary productivity can be measured in terms of biomass as grams per square meter per year (g/m²/yr). Alternatively, the caloric content of the biomass can be measured and net primary productivity reported as calories per square meter per year. Since the rate of vegetation growth varies in different ecosystems, net primary productivity is highly variable from place to place. In general, plant biomass and primary productivity are highest in the warm and wet tropics and lowest in cold polar ecosystems and dry deserts. The mean net primary productivity of a tropical rainforest ecosystem is some 2200 grams per square meter per year. In desert environments, the net primary productivity averages from 90 to 3 grams per square meter per year. The net primary productivity of the open ocean averages 125 grams per square meter per year. We will discuss the global distribution of net primary production further when we examine the world’s biomes.

When we look at the distribution of the standing biomass of different trophic levels, the impact of the 10% rule quickly becomes apparent. These distributions often have a pyramidal shape in which biomass can decrease by 90% or more with each increase in trophic level. However, the shape of such pyramids can vary widely. In Panamanian rainforests, it has been shown that it takes approximately 40,000 grams per square meter of vegetation biomass to support
14 grams per square meter biomass of primary consumers, secondary consumers, and decomposers. In coral reef systems, 703 grams per square meter of primary producer biomass can support 132 grams per square meter of herbivores and 11 grams per square meter of carnivores.

It would therefore seem that we should be able to predict the number of trophic levels that a given ecosystem will support. The food webs of insects, which have high-energy efficiencies, living in ecosystems with high primary productivity should contain more trophic levels than other types of communities. Interestingly, this has not been found to be the case. Most terrestrial food webs, despite differences in primary productivity and the thermal efficiency of the organisms, tend to have three to four trophic levels. This means that energy flow cannot be the only factor limiting the number of trophic levels. It is also interesting to note that despite the low primary productivity of the oceans, many marine communities have five trophic levels, and carnivores are much more abundant compared to the number of carnivores found in terrestrial systems. It is possible that the transfer of energy between the marine primary producers, which are mostly microscopic plants that float in the water, and primary consumers, which are mainly microscopic crustaceans called copepods, is much more efficient than the transfer of energy between land plants and terrestrial herbivores. Indeed, in some oceans the standing biomass of photosynthetic plankton may be low relative to the biomass of other trophic levels because of the efficiency with which the copepods harvest the phytoplankton and incorporate the energy captured by them. In the English Channel, 21 grams per square meter of herbivore standing biomass are supported by only 4 grams per square meter of primary producer standing biomass.

As a final thought on trophic levels, we might reflect on the place of humans in the food webs of the world’s ecosystems. Since we are omnivores, we function as both primary consumers and higher level consumers. It is easy to see that when we eat the meat of herbivores such as cows or sheep, we are secondary consumers. When, however, do we function as tertiary or quaternary consumers and eat other carnivores? Most people eat fish. Important food species such as tuna and salmon are carnivorous tertiary and quaternary consumers. Thus, in terms of marine food webs, we function as quaternary consumers or even higher in the trophic hierarchy!

**PHYSICAL GEOGRAPHY AND THE FUNCTIONING OF THE EARTH**

The science of physical geography is concerned with the physical patterns and processes that occur at the earth’s surface. Physical geographers conduct research on phenomena ranging from local landforms caused by glacial activity to large-scale variations in the world climate. The most important areas of physical geography for biogeographers are climatology, which is the study of the earth’s atmosphere and climate; pedology, which is the study of soils; limnology, which is the study of freshwater; and oceanography, which is the study of the world’s oceans. It is worthwhile to review a few important concepts from the areas above in order to investigate how features of the earth’s physical environment interact with the biosphere to influence the distribution of life.
Global Climate

Before we begin our examination of the earth’s climate, we should note the difference between the terms weather, climate, and atmosphere. These are three very different concepts and are sometimes confused. Weather is the condition, or physical state, of the atmosphere at a given place at a given time. The weather changes from day to day or even hour to hour. Climate is the average condition of the atmosphere at a given place based on statistics from a long period of weather observations. When someone says it is raining in Boston today, he is describing the weather. When you read that the average temperature in Los Angeles in July is 25°C, you are reading a description of climate. By convention, such climatic averages are usually based on 30 years of observation.

The atmosphere is the layer of gas that surrounds the earth. The atmosphere extends over 100 km above the surface of the earth and is divided into several different layers based on temperature, pressure, and chemical composition (Fig. 2.4). However, all life exists in the lowest level of the atmosphere, called the troposphere. The troposphere extends some 9 to 17 km above the earth and contains over 90% of the total mass of the atmosphere. The composition of pure dry air in the troposphere is roughly 78% nitrogen, 21% oxygen, 0.93% argon, and 0.036% carbon dioxide and a small amount of other gases. The air in the troposphere can be relatively dry or contain up to 5% water vapor in places such as the humid tropics. Both air pressure and temperature decrease with height in the troposphere. For every 275-m rise in elevation, the air pressure decreases by about 3.3%, while temperature decreases at a rate of approximately 6.5°C for every 1000-m increase in altitude. This is why the air is thinner and temperatures are cooler at the tops of high mountains.

As you recall from our discussion of photosynthesis, most of the sunlight received by the earth is in the visible light portion of the electromagnetic spectrum (~0.4–0.6 micron wavelength). This energy is absorbed at the earth’s surface.

![Figure 2.4](image-url)
and then emitted as heat energy at longer wavelengths of ~5.0 to 20.0 microns. The gases of the atmosphere allow most of the solar energy in the visible light wavelengths to pass through the atmosphere but tend to absorb the longer wavelength heat energy that is emitted from the earth’s surface. Carbon dioxide and water vapor in the atmosphere are important in trapping this heat. This phenomenon of the transmission of incoming solar light energy and the trapping of outgoing heat energy is known as the greenhouse effect. Without this atmospheric effect, the earth would be too cold to support life.

The distribution of climatic conditions on the earth is not random but follows a predictable pattern that is controlled mainly by latitude, elevation, and the distribution of continents and oceans. As we shall see later, if we can predict the climatic conditions at a certain place, we can also make certain predictions about the type of organisms we will find there. Latitude is the most important control on the overall distribution of climatic conditions. Latitude determines the amount of solar energy that is intercepted over a given area of the earth’s surface (Fig. 2.5). The earth orbits the sun at an average distance of about 150 million km. The orbit is elliptical, so that in January the earth is about 2 1/2 million km closer to the sun. This is referred to as the perihelion. The aphelion occurs in July when the earth is an additional 2 1/2 million km away from the sun. At these distances, the electromagnetic energy from the sun can be assumed to be traveling as parallel waves with a constant energy of 1400 watts per square meter. During March and September, at the equator, these rays strike the earth at a 90° angle at noon, so that a square meter of incoming solar radiation is intercepted by a square meter of earth’s surface. At higher latitudes, the angle of incidence of the sun’s rays decreases. As a result, a square meter of solar energy is spread over an area much greater than a square meter of the earth’s surface. Due to the decrease in the angle of insolation, temperatures should be cooler at higher latitudes because they receive less solar energy. However, that is only part of the story.

The latitudinal distribution of solar energy varies with season as well as latitude. Because the earth’s axis is tilted about 23 1/2° relative to the plane of the orbit around the sun (Fig. 2.5), the amount of solar energy received at different latitudes varies throughout the year. At the December solstice, the northern hemisphere is tilted away from the sun so that the angle of incidence of solar energy is decreased and areas north of 66 1/2° (the Arctic Circle) do not receive any direct sunlight. The point of the earth’s surface where the sun’s rays strike the earth at a 90° angle lies at 23 1/2° south latitude (the Tropic of Capricorn). During June and the summer months, the northern hemisphere is tilted toward the sun, and the angle of incidence in the north is increased. North of the Arctic Circle the sun never sets. The sun’s rays strike the earth at a 90° angle at the Tropic of Cancer (23 1/2° north latitude). The tropics are defined as the region lying between 23 1/2° north and south latitude. During the equinoxes, on March 21 and September 23, the axis of the earth is perpendicular to the plane of its orbit. The sun’s rays strike the earth at a 90° angle at the equator, and there are 12 hours of daylight at all latitudes.

The seasonal distribution of insolation has important implications for temperatures and life on earth. The long days of insolation during May, June, July, and August at the high latitudes of the northern hemisphere provide large amounts of solar energy. This energy results in temperatures warm enough for ice and snow to melt and plant life to exist. In the southern hemisphere, the long days of high insolation are experienced in the months of November, December, and January. Thus,
during the 24 hours of sunlight in June, the North Pole actually receives more insolation than the equator (Fig. 2.5). However, over the course of the year, the average insolation at the equator is much higher than at polar regions. A very important additional aspect of insolation distribution is the way that seasonal differences increase with latitude (Fig. 2.5). Organisms existing in the Arctic and Antarctic polar regions not only have to contend with less total insolation, but they have to adapt to large seasonal differences between winter and summer. A final interesting point to note, is that the high and midlatitudes experience one insolation peak during the summer, while the equator experiences two peaks in spring and fall.

If incoming insolation was the only control on temperatures at the surface of the earth, we would see surface temperatures decreasing in a smooth fashion, parallel with latitude, from the equator to the poles. However, if we look at maps of mean January and July temperatures, we see that temperatures do not decrease smoothly in parallel with latitude (Fig. 2.6). Some of this can be explained by differences in elevations. As we discussed earlier, high-elevation sites are cooler on average than low-elevation sites. Upon inspection of temperature maps, it is clear...
that summer temperatures are higher over land surfaces than over the sea. Winter temperatures are lower on land relative to the sea. This phenomenon is particularly noticeable in interior Alaska and central Siberia where average January temperatures range from $-25^\circ C$ to $-50^\circ C$, while January temperatures in the adjacent North Pacific range from $0^\circ C$ to $-15^\circ C$. In fact, central Siberia is the coldest place in the northern hemisphere, with winter temperatures commonly far below those encountered at the North Pole. The coldest recorded temperature in North America occurred in the village of Snag in the Yukon Territory of Canada. In July the average daily temperatures in Siberia and Alaska rise to $10^\circ C$–$15^\circ C$, while the air temperatures over the oceans increase to only $5^\circ C$–$10^\circ C$. The reason for these differences in surface temperatures of continents and oceans is related to the differential rates of heating and cooling of land and

**FIGURE 2.6** Average monthly temperatures ($^\circ C$) at the surface of the earth in January and July (after Strahler and Strahler, 1997).
The solid land surface heats and cools more rapidly than the liquid sea where energy is dispersed in depth. Thus, the land responds more dramatically to the seasonal increases and decreases in insolation. In addition, the oceans circulate heat laterally through currents. Such transfers do not occur on solid land surfaces. Sites that are located in the interior of landmasses and are subject to dramatic seasonal differences in temperature are said to experience continental climates, whereas islands and coastal sites, that have climates moderated by the ocean, are said to have marine climates. In the case of Siberia, the difference between the mean January and July temperatures can be as high as 60°C. In the interior of Alaska and Canada, this difference in seasonal mean temperatures is about 45°C. In contrast, the difference between January and July temperatures on islands and at coastal sites in the tropics is less than 3°C.

Now, let's consider the geographic distribution of precipitation. The term precipitation is used here to denote moisture that is deposited from the atmosphere to the land or water surface as rain, sleet, hail, or snow. Precipitation occurs when the water vapor in the atmosphere exceeds the moisture-holding capacity of the air. The amount of water that can be held as vapor increases rapidly with air temperature. Air with a temperature of 0°C can only hold about 5 g of water per kilogram of air, whereas air with a temperature of 30°C can hold over 25 g of water per kilogram of air. When air cools, its ability to hold moisture as vapor decreases and eventually precipitation forms. As we discussed, air generally cools with increasing altitude in the troposphere. The average rate of temperature decrease is about 6.5°C for every 1000 m of altitude, although this varies. Air that is relatively dry cools at a rate of about 10°C per 1000 m. This is called the dry adiabatic lapse rate. Air in which condensation is occurring cools at the wet adiabatic lapse rate, which is approximately 3°C per 1000 m. So, as air rises it cools, and if it cools enough, condensation and precipitation occur.

Three processes cause air to rise and generate precipitation. The first process is convective precipitation, which occurs when the warming of air at the surface causes the air to rise until it becomes cool enough for precipitation to occur. This phenomenon causes the thunderstorms and rain showers typical of summer weather in many parts of the world, particularly the tropics. The second process is frontal precipitation, which occurs when warm air masses rise up and over denser masses of cool air. An example of this phenomenon are the winter storms that occur in the middle latitude regions. Finally, air may be forced to rise when it encounters physical barriers such as mountains. Rain generated in this fashion is referred to as orographic precipitation. The high rainfall encountered on the western slopes of the Coast Ranges from northern California to Alaska is influenced by orographic conditions.

The global distribution of precipitation is controlled by surface conditions, such as the location of mountains and oceans, and by the general circulation of the atmosphere. The general circulation of the atmosphere is the large-scale patterns of winds that develop in response to differences in radiation and heat at the equator and the poles. Precipitation, due to convection, is typical of the equatorial regions which, due to high insolation, experiences vigorous heating at the earth's surface. This surface heating causes air to warm and rise. High rates of evaporation from the warm sea surface provide abundant moisture to the atmosphere. At approximately 30° north and south latitude, the tropical air begins to subside and warm as it descends (Fig. 2.7). As the air warms, it can carry more water as vapor. Thus, areas that are typified by descending air are dry. The descending air causes a
band of calm and dry climate in the subtropics at around 30° north and south latitude. These regions are referred to as the doldrums or horse latitudes because sailing ships often were becalmed in these latitudes and the sailors would jettison horses and other livestock to conserve water. At the surface, air flows from the region of the horse latitudes to replace the rising air in the tropics (Fig. 2.7). The flow of the air is deflected to the right due to the Coriolis effect imparted by the rotation of the earth. As a result, there is a zone of winds from the northeast and the southeast in the equatorial region that are referred to as the tropical trade winds. The region where the trade winds from the northern and southern hemisphere converge is called the Inter-Tropical Convergence Zone (ITCZ). The converging winds at the ITCZ replenish moisture for convective precipitation in the tropical zone. North and South of the horse latitudes, the surface air flows away from the zone of subsidence in an easterly direction, and this is referred to as the midlatitude westerlies. These westerlies dominate the temperate areas of the earth between 30° and 60° north and south latitude. Storms develop along the belt of westerlies as the atmosphere picks up moisture over the oceans and produces frontal precipitation. North and south of the midlatitude westerlies, polar air masses dominate. The polar air masses are generally very cold and very dry.

Elevation also plays a role in the distribution of precipitation. Because of orographic lifting and cooling of air, high elevations typically have higher amounts of precipitation than adjacent low-elevation sites. In areas such as coastal Oregon, Washington, and British Columbia, the frequent occurrence of midlatitude frontal storms brought ashore by the westerlies, coupled with orographic precipitation due to high mountain ranges along the coast, produces large annual totals of precipitation. Air also heats as it descends down the lee side of mountains. This promotes dry conditions, which are referred to as rainshadows. In the region of westerlies, rainshadows are often found on the east side of mountain ranges. The dry eastern slopes and the adjacent deserts of the Sierra Nevada Mountains of California are a result of the rainshadow effect. The warm and dry winds, experienced as air flows down mountains, are called Chinook Winds in the northern Rocky Mountains and Fohn Winds in Europe.

The general distribution of annual precipitation on the earth reflects the processes outlined above (Fig. 2.7). The greatest amounts of precipitation generally occur in the tropics where over 500 cm of rainfall may fall in a given year. Similar magnitudes of rainfall are experienced on the western slopes of coastal mountains in western North America, Norway, and western South America. A band of low precipitation is centered on 30° north and south latitude. This includes some of the world’s great deserts such as the Sahara in northern Africa, the Namibian in southern Africa, the Arabian Desert, the coastal deserts of Chile and Peru, the Australian Outback, and the deserts of the U.S. Southwest and adjacent Mexico. Average annual rainfall in some of these regions may be less than 2.5 cm per year. In some areas, such as the Sahara Desert of southern Sudan, 100 years may pass between occurrences of measurable rainfall. In the midlatitudes, very dry conditions and deserts may extend as far as 45°-50° north and south latitude in the rainshadows of mountain ranges. The Great Basin Desert of California, Nevada, and Utah is an example. The arctic and antarctic regions also experience low annual precipitation. However, we generally do not think of these regions as deserts. Low precipitation is not the only factor in creating a desert. In true deserts, the rate of evaporation greatly exceeds precipitation, and there is a deficit in soil moisture at most times. The arctic and antarctic regions have low precipitation, but because of low temperatures,
FIGURE 2.7 General circulation of the atmosphere and average annual precipitation (after Strahler and Strahler, 1997).
they also have low evaporation rates. Therefore, these polar regions cannot be considered to be true deserts in most cases.

In addition to geographic variations due to latitude and orographic features, seasonal differences in precipitation are important influences on the distribution of life. The ITCZ does not stay fixed at the equator but changes seasonally. During June and July the ITCZ moves north toward 23 1/2° north latitude. During December and January it moves toward 23 1/2° south latitude. As the ITCZ moves north and south, it brings precipitation to the arid subtropical regions near 30° north and south latitude. In addition, the increased warming of the land surface in the subtropical regions during the summer produces a pattern of enhanced convective uplift over the land and surface flow of moist air from the oceans. This creates a rainy season called the Summer Monsoon, which is important for bringing moisture to areas such as India, Southeast Asia, and the Southwestern United States. Thus, the areas bordering the tropics experience their highest rainfalls during the summer months and often have very dry winters. In the midlatitudes, the westerly storm tracks are also displaced. In the summer, westerly storms do not generally travel as far south as California or Spain, and this brings dry summers to these regions. In contrast, during December and January, the storm tracks move south and bring winter rains.

Because of geography’s role in controlling temperature and precipitation, the earth can be divided into broad climatic zones based on temperature and precipitation regimes. One such scheme, often used by biogeographers, is based on the 1918 work of Wladimir Köppen as later modified by Geiger and Pohl. Köppen was a knowledgeable biogeographer as well as a climatologist, so his system was designed to reflect the relationship between world climate and vegetation zones. The climatic zones he proposed are based strictly on long-term climatic averages. In determining the boundaries of the climatic zones, Köppen also used vegetation boundaries as guides. He reasoned that large-scale vegetation boundaries were likely related to climate. The complete Köppen system has 5 major climate zones and 13 climate types, with a mechanism for further subdivisions. A simplified global version of the Köppen system excluding highland areas is presented in Figure 2.8. The five major climate zones are:

A. Tropical Rainy Climates found in the equatorial regions. This zone has monthly average temperatures of 18° C or higher, with little seasonal variation. Rainfall is abundant throughout the year and always exceeds evaporation.

B. Dry Climates found mainly in the subtropical zone. Temperatures are generally warm, and evaporation exceeds precipitation throughout all or most of the year.

C. Mild Humid Climates found in the midlatitudes. The temperature of the coldest month falls between 18° C and –3° C, with a clear difference in winter and summer seasons. Precipitation exceeds evaporation.

D. Snowy Climates found in the mid- to high latitudes. The coldest month has an average temperature below –3° C, but the average for the warmest month is greater than 10° C. Precipitation exceeds evaporation.

E. Polar Climates found in the polar regions. The average temperature of the warmest month is less than 10° C. Precipitation is low, but evaporation is very limited.
Before we conclude this review of climate, we will consider some interesting properties of local climate related to mountains. Under normal conditions, temperatures decrease with altitude. Thus, high elevations are generally cooler than low elevations. The impact of this can be seen with particular clarity when we consider how the high elevations of mountains such as the Appalachians or Alps experience lower temperatures than the adjacent lowlands during both the summer and winter. However, in some localized instances, valley bottoms in the mountains can experience colder temperatures than the surrounding slopes and peaks. The enhanced cooling of the valleys is caused by dense cold air which drains downward from higher elevations, particularly at night and in the early morning. The effect is known as cold air drainage. In some instances, valley bottoms may be too cold to support trees, which grow well on adjacent slopes.

**Microclimate**

In our discussion we have looked at relatively large-scale climatic conditions. However, significant differences in climate can occur at very small scales. Such very local conditions are referred to as microclimates. For example, aspect is the direction that a slope faces. A south-facing slope in North America can experience daytime temperatures that are over 10°C warmer than an adjacent north-facing slope. Evaporation rates are also higher on the warm south-facing slope, so soils are drier. Thus, the south-facing slope may support plants and animals that are typical of hot and dry climates, such as desert species, while the adjacent north-facing slope may be wooded. South-facing slopes in the Yukon Territory of Canada sometimes support plants typical of the northern Great Plains, while adjacent north-facing slopes support cool subarctic forest species. Sites close to the ground are generally warmer than elevated and exposed sites. In the arctic, summer daytime temperatures can decrease by over 5°C from the soil surface to 30 cm above the surface. Temperatures decrease rapidly below the soil surface.
The air temperature in rodent burrows, which are only a few tens of centimeters below the surface, may be over 10° C cooler than the exposed top soil.

Forests create profound differences in microclimate. The amount of sunlight received at the floor of a dense forest may be less than 10% of the amount received at the top of the forest canopy. Temperatures at the forest canopy can be well over 10° C higher than those found on the forest floor. Decreased evaporation rates and the transpiration of leaves cause forest floors to be much damper than at the canopy level. Finally, wind speed can decrease by as much as 90% between the top of the canopy and the forest floor.

World Soils

Soil is the uppermost layer of mineral and organic matter found on the earth’s surface. Soil supports and sustains almost all plant life on which terrestrial ecosystems depend. In addition, many organisms, ranging from bacteria to mammals, live within the soil. Soil structure, texture, mineralogy, water content, and chemistry can exert a strong control on the distribution of organisms. Soil is formed by the physical and biological weathering of rock and the addition of organic matter. The formation of soils is dependent on many factors and can take thousands of years. The type of regolith (weathered rock and mineral matter) from which soil is developed is important. Plants and animals may depend on soils, but they also modify regolith to create soils. In this manner soil and life on the earth have evolved together. Climate is also extremely influential in determining the type of soil that will develop in a given locale. Both temperature and moisture conditions can have a great influence on soil development. Thus, soils vary in structure, texture, and chemical properties both locally and globally. A gradient in soil characteristics and types across landscapes is referred to as a catena.

One means of describing soils is by texture. This refers to the amount of sand, silt, and clay in the soil. Loam soils, with a relatively equal mixture of silt, sand, and clay, are often best for plant growth because they hold and exchange water easily and provide mineral nutrients in a form useful to plants. Water runs quickly through sandy and rocky coarse soils. In addition, plants cannot obtain nutrients from coarse particles. Water runs slowly through clay-dominated fine soils and is difficult for plants to acquire. Clay and silt soils that lack sand can impede root penetration.

Soils can be divided into stratigraphic units called soil horizons. The boundaries between the horizons generally run parallel to the soil surface. Each horizon has distinctive physical and chemical properties. Often, color can be a useful means of discriminating soil horizons and different soil types in the field. An objective means of describing soil color is provided by the use of a standardized color chart provided by a Munsell Color Book. A vertical section through the various horizons is called a soil profile, and comparing profiles provides another means of classifying soils. The principal horizons of a soil profile are generally designated as A, E, B, and C (Fig. 2.9).

The C horizon is the unconsolidated rock at the base of the soil profile. It can retain traces of the structures and bedding of the original rock. The C horizon has undergone little chemical transformation and most closely resembles the chemical and mineral composition of the original rock. However, silica, carbonates, and salts, weathered from the overlying horizons, can accumulate in the C
horizon. The base of the C horizon is often difficult to determine exactly as it grades into the unweathered underlying rock.

The B horizon overlies the C. It is highly weathered and does not retain any traces of the original bedding or structures of the bedrock. The B horizon is typified by illuviation (the accumulation of material) and contains substances such as clays, calcite, aluminum and iron oxides, and humus (organic matter) that have been weathered and leached downward from the overlying horizons. Some of these substances bind particles together, imparting structures of granules, plates, blocks, and columns to the B horizon. Under certain conditions the accumulation of iron oxides, gypsum, salts, silica, and clay can form impermeable layers that block the movement of water and nutrients in the soil profile. When such barriers
consist of uncemented clays, they are called fragipans or claypans. When they consist of cemented material, they are called duripans or hardpans.

The A and E horizons are formed by eluviation (loss of material) and are depleted in clays, aluminum, and iron oxides relative to the B horizon. When leaching is particularly intense, the E horizon can be bleached of color, while organic matter in the A horizon makes it darker. Because biological activity such as rooting and soil-dwelling organisms is important, the A horizon contains more humus than the E. The A horizon can consist of up to 30% humus. The decay of humus releases organic acids that promote weathering and leaching in the soil. The replacement of cations such as calcium, magnesium, potassium, and sodium in the A and E horizons by hydrogen can reduce the ability of the soil to support plant growth. In some cases an extremely organic-rich layer of plant matter, the O horizon, overlies the A horizon.

As is the case with climate, the soils of the world can be classified into broad categories to produce world soil maps. The pioneers in the area of soil description, classification, and mapping were the Russian scientists V. Dokuchaev and K. Glinka and Americans such as E. Hilgard and C. Marbut who worked in the late nineteenth and early twentieth centuries. Broad classification systems take into account the structure, texture, chemical properties, and profiles of the soils. Unlike biological taxonomy, however, there is no international standard system for the classification of soils. Even in North America different systems are used. In the United States the Comprehensive Soil Classification System is the accepted norm. Canada has a different system, the Canadian System of Soil Classification. Many other countries have developed their own systems or use terms from world soil classification schemes developed by Russian or British pedologists.

The Comprehensive Soil Classification System divides soils into 11 soil orders. The different orders are discriminated on the basis of criteria such as soil composition and texture, degree of horizon development, presence or absence of diagnostic horizons, and degree of weathering of soil minerals. The global distribution of these soil types has been mapped by the U.S. Department of Agriculture (Fig. 2.9). The distribution of some soil types do correspond with Köppen’s climatic regions. The soil orders are as follows:

**Entisols** are mineral soils that have undergone little to no alteration. They lack distinct soil horizons and are often found on fresh deposits from rivers, glaciers, and sand dunes. Because of low weathering, it may be difficult for plants to obtain nutrients from some entisols. Many tundra and desert soils are entisols.

**Inceptisols** are young soils that possess enough soil moisture to support plants for at least three months of the year, have one or more discernible horizons, are fine to loamy in texture, and contain weathered minerals and associated plant nutrients. Some tundra soils are inceptisols. Cryaquept inceptisols are typically found in polar climate regions and high mountains. Aquept inceptisols are found in bogs and marshes throughout the world. Inceptisols are also found on floodplains where significant sedimentation is no longer occurring.

**Histosols** are generally moist and have up to 30% organic matter in the upper portion of the soil. The organics can come from mosses and other plants growing in water, such as in bogs, and from deep forest litter. These soils are
commonly acidic and low in nutrients. High water content may produce reducing conditions and an abundance of iron oxides in the mineral soil beneath the A horizon. Histosols are common in the coniferous forests of the snowy climate region. They can also be found in other regions on wet, vegetated sites.

**Oxisols** are characterized by the deep weathering of most minerals except quartz, aluminum, and iron. The soils have water, but the nutrient content is often low. They generally present little evidence of soil horizons, except that the surface is darker owing to the presence of organics. Hard concretions (plinthites) and layers (laterites) of iron concretions form in oxisols. Oxisols are found in the warm and moist areas of the tropical moist climate zone.

**Ultisols** have a prominent E horizon and a B horizon in which clay minerals accumulate and can form plinthite. These soils are low in plant nutrients. The mean soil temperature for formation of ultisols is 8°C, and they are associated with climates that produce an abundance of moisture in one season and dry conditions during another.

**Vertisols** have a high content of clay and shrink and swell depending on water content. They have cracks and other evidence of soil movement. Soil horizons may not be apparent. These soils have good nutrient availability but are difficult to work for agriculture. Vertisols form under grassland and savanna vegetation in the tropical and subtropical regions.

**Alfisols** have a gray to reddish horizon close to the surface that lack darkening by humus and an underlying layer of clay accumulation. Alfisols have good nutrient compositions for plants. Alfisols form under forests (Boralfs and Udalfs) and mixed forest-grassland, shrub cover (Xeralfs and Ustalfs) at sites ranging from the conifer forest in the snowy climate region to seasonally dry sites in the midlatitudes and subtropics.

**Spodosols** often have a bleached and light-colored E horizon that overlies a dark layer of illuviated humus, aluminum, and iron in the B horizon. Spodosols are generally acidic and low in nutrients. In many cases these soils are relatively young, despite the clear development of horizons. They are found under coniferous forests in the snowy climate zone.

**Mollisols** have a very thick and dark A horizon with a soft structure. Vertical cracks form in the soils due to cycles of wetting and drying out. These soils have high amounts of calcium and generally high nutrient content. Mollisols are perhaps the most fertile soils in the world. They form under grasslands in the dry climate regions of the midlatitudes.

**Aridisols** are dry soils that have low humus content but clear horizons. They can have high amounts of calcium and salt layers. They form in the arid climate zone where water content in the soil is too low to support much plant growth.

**Andisols** are soils formed on fresh deposits of volcanic ash. They have a small geographic distribution and can be very fertile.

**The Physical Environment of Lakes**

Lakes cover about 2% of the earth’s surface and contain only about 0.01% of the world’s water. However, lakes provide habitats for many types of plants,
invertebrates, fish, amphibians, birds, and mammals and are an important focus of biogeographic research. Lake basins can be formed by a number of natural processes, including glacial activity, volcanic activity, tectonism, landslides, changes in river channels, and changes in ocean shorelines. Differences in light, temperature, acidity, and the chemical composition of water produce different physical environments in different lakes and within the same lake. These differences can have a profound impact on the geographic distributions of lake-dwelling organisms.

Aquatic organisms are sometimes classified by their habitat. Plankton are organisms that exist by passively floating in the waters of a lake or ocean. These include many microscopic plants (phytoplankton) and small invertebrate animals (zooplankton). Organisms such as fish that can propel themselves through the water are referred to as nekton. Finally, benthic plants and animals are those that exist on the bottom of lakes and oceans. The water environment is called the pelagic zone, while the bottom is called the benthos.

Plants that live in lake waters require sunlight for photosynthesis. When sunlight from the PhAR portion of the electromagnetic spectrum strikes the surface of a lake, some of it is reflected directly back skyward and does not enter the water. When light strikes the water at a 90° angle, only a small percentage of the energy is reflected. However, at a 10° angle, about 40% of the light is reflected off the lake waters. Once the light enters the water, its energy is dispersed by absorption and scattering. The transmission of PhAR is optimal in clear distilled water. In such water, light in the blue wavelength is transmitted best. Longer wavelength light, from the red portion of the spectrum, transmits poorly. About 53% of the light is absorbed and emitted as heat in the first meter or so of the water. However, lakes do not contain pure distilled water. Instead, their waters contain suspended and solid organic and inorganic substances and organisms such as plankton. The more matter and organisms in the lake water, the less light that can be transmitted through the water. In small, productive lakes with high amounts of suspended matter and organisms, the water is murky, and little light is transmitted below the first meter of water. In large, low-productivity lakes, such as Lake Tahoe in California or Crater Lake in Oregon, significant amounts of light can be transmitted tens of meters through the clear water. However, at greater depths, most of the light that is transmitted is in the blue portion of the spectrum. The portion of the lake water column that receives sufficient sunlight for photosynthesis is called the euphotic zone. Depths beneath this that receive enough light for fish and other organisms to see, but not enough for sustained photosynthesis, are referred to as the disphotic zone. Depths that are totally dark are called the aphotic zone. Photosynthetic plants can only live in the photic zone. Sometimes limnologists classify parts of lakes according to their ability to support photosynthetic plants. The shallow margins of the lake where plants can root and receive adequate light for photosynthesis is called the littoral zone, while the deep dark portion where rooted plants cannot exist is called the profundal zone (Fig. 2.10).

The impact of solar radiation coupled with warm air temperatures in the summer often produces a thermal stratification where temperatures are higher in the upper waters. Mixing of the surface waters by winds and currents generates isothermal conditions in the upper few meters of the lake waters. Below this, there is a gradient of decreasing temperature called a thermocline. At depth, the lake waters are cool and isothermal (Fig. 2.10). The difference in temperature between the surface and bottom waters can be as much as 20° C in relatively
deep lakes. If you have dived and swam in small northern lakes, you may have experienced this thermal gradient as a feeling of increasing chill below a certain depth. These three thermal zones are called the epilimnion, metalimnion, and hypolimnion, respectively. The metalimnion produces a thermal barrier, and there is little mixing of waters from the epilimnion with the hypolimnion. Among other things, this phenomenon affects the distribution of oxygen. There are relatively high amounts of dissolved oxygen in the epilimnion and low amounts in the hypolimnion (Fig. 2.10). In some cases the bottom waters are anoxic and cannot support organisms that require oxygen for respiration. This stratification of temperature and oxygen breaks down seasonally in lakes located in cold regions and allows oxygenation of bottom waters. Some lakes that are deep relative to their surface area never experience oxygenation of bottom waters.

The degree of thermal stratification in lakes can be related to the relationship between lake area and depth and climatic conditions—particularly air temperatures. This provides a means of lake classification linked to climate:

- **Amictic Lakes** never lose their cover of ice and do not stratify. They are found only in the antarctic, a few places in the arctic, and on very high mountains.
- **Cold Monomictic Lakes** never exceed 4° C water temperature and do not usually stratify. These lakes are found in the polar regions and on high mountains.
- **Dimictic Lakes** are the stratified type described in the preceding discussion. They stratify in summer and mix in spring and fall.
- **Warm Monomictic Lakes** never have water temperatures below 4° C. They stratify directly in summer. They are found in warm temperate areas and subtropical mountains.
- **Oligomictic Lakes** have water much warmer than 4° C and irregular circulation events. There may be little temperature difference between the epilimnion and hypolimnion. These lakes are found in tropical regions.
Two categories of lakes can be found in both warm and cold climates.

**Polymictic Lakes** are shallow and circulate continuously.

**Meromictic Lakes** are deep lakes in which the bottom waters remain unoxygenated, even during lake overturn.

Lakes can also be classified in terms of chemistry, nutrient status, and productivity. Many lakes have freshwater; however, some saline lakes contain salt concentrations that are as high or higher than that of the ocean. Such saline lakes, generally develop in arid regions and basins that lack outlets. Water is lost from these lakes mainly through evaporation, resulting in the accumulation of salts. Deep, cold lakes, with high amounts of oxygen and low amounts of phosphorus and other nutrients, typically have low primary productivity. These are referred to as oligotrophic lakes. In contrast, shallow, warm lakes, with high amounts of nutrients have high primary productivity. These are called eutrophic lakes. However, eutrophic lakes generally have low amounts of oxygen due to high rates of respiration and aerobic decomposition. In some cases, the oxygen levels can decrease to the point where catastrophic die-offs occur for fish and other organisms.

**The Physical Environment of Oceans**

About 71% of the earth’s surface is covered by ocean. This, coupled with the depth of the ocean, provides an area of habitat for marine life that is 300 times greater than the area provided by the terrestrial surface of the earth.

As is the case with freshwater, light does not penetrate far down in ocean waters. In marine waters near the shore, sunlight may only reach the upper few meters of the water column. In clear midocean sites, light can penetrate many tens of meters, and 1% of the incident light may reach depths of 150 m. Photovoltaic plants such as microscopic phytoplankton, or large plants such as kelp, can exist only in this upper photic zone. So, despite its great depth and volume, the marine environment must depend on a thin surface layer for its primary productivity.

As is the case with lakes, the ocean environment can be divided into pelagic and benthic zones (Fig. 2.11). In addition, in the sea the pelagic environment is subdivided into a nearshore neritic zone that extends to the edges of the continental shelves and a deepwater oceanic zone. The pelagic zone is also subdivided by depth into five regions (Fig. 2.11). All photosynthesis takes place in the uppermost epipelagic environment. Because the water is clearer in the midocean areas, the photic zone is deeper there than it is near the continents. Light sufficient for photosynthesis may penetrate for well over 10 m in the mid-ocean. The benthos of the ocean is also subdivided into a number of subzones extending from the intertidal supralittoral to the very deep hadal. The substrate of the benthos is very important in determining the organisms that can live there. Substrate varies by depth and proximity to land. Shallow areas near the shore may have substrates ranging from rocks, gravel, sand, and living coral. Areas in the deep sea away from land and the continental shelves, often have substrates dominated by very fine silt and clay sediments.

A major difference between the marine environment and the freshwater environment of lakes and rivers is salinity. In general, the salinity of the ocean is about 35 g of inorganic salts per 1 kg of sea water, the major salt being sodium.
chloride. However, the concentration of salts varies with both latitude and depth. In general, the salinity of surface waters is greatest in the regions between 20° and 40° north and south latitude where evaporation rates on the ocean are high relative to precipitation (Fig. 2.12). This corresponds with the dry climatic zone of terrestrial deserts discussed previously. In addition, in the low and midlatitudes, salinity decreases with depth between the surface and about 1000 m. Below 1000-m depth, the salinity remains fairly constant.

The temperature of the ocean is an important control on planktonic and shallow nektonic organisms. As we might suspect, sea surface temperatures (SSTs) are highest in the low-latitude regions and decrease poleward (Fig. 2.12). Water temperature also varies with depth, and where the surface waters are relatively warm, a thermocline is usually found between the surface and 1000 m depth. Deep waters are not prone to seasonal changes in temperature. Waters below 2000 to 3000 m never rise above about 4°C, and in the deepest portions of the ocean water temperatures can be below 3°C. In the deep ocean waters, there is little temperature difference between the equator and the poles.

Oxygen in the oceans is highest in the surface waters and declines to minimum values at 500 to 1000 m depth. In some cases, oxygen concentrations may drop close to zero. The oxygen minimum zone is attributed to high rates of biological activity such as respiration and decomposition coupled with a lack of oxygen replenishment by photosynthesis because of the absence of light at this depth. Below the oxygen minimum zone, oxygen then increases with depth (Fig. 2.11). However, in some cases, such as off the coast of Santa Barbara, California, the sea bottom may be permanently anoxic. In other cases, such as the Gulf of Mexico, seasonally anoxic conditions may develop on the ocean floor.

The oceans display complex surface current systems that are largely driven by winds and the impact of the Coriolis effect (Fig. 2.12). Such systems work to bring warm waters poleward and moderate climates in areas such as northern Europe and western Alaska. These currents are also an important means for dispersing plankton and aiding in the migration and dispersal of nektonic organisms. In addition to surface currents, subsurface currents produce upwelling zones where cool nutrient-rich waters rise from depth to provide zones of high oceanic
FIGURE 2.12  Ocean surface temperatures, salinity, currents, and major upwelling zones (from a number of sources including Lalli and Parsons, 1997; Ross, 1992; Thurman, 1990).
productivity (Fig. 2.12). Fisheries in areas such as coastal California owe their high catches to such upwelling.

A final important physical factor controlling the distribution of life in the oceans is pressure. Because the oceans are so deep, there are great differences between the ambient pressure that is exerted on organisms at the surface and pressure in the hadal zone. Pressure is determined by the weight of the overlying water. Ocean pressure is measured in atm units (atmospheres). One atm equals the average pressure of the atmosphere at sea level. The pressure of the ocean increases by 1 atm for every 10 m of depth. So, in the deepest parts of the ocean, at 11,000 m, the weight of water is equal to 1100 times the atmospheric pressure we experience at sea level. These pressures present special challenges for organisms that contain gas-filled sacks such as the swim bladders of fish or the lungs of marine mammals. In addition, pressure makes the exploration or collection of the biota of these depths extremely difficult. This is why the depths of the ocean represent one of the great unexplored frontiers of biogeography.

**KEY WORDS AND TERMS**

<table>
<thead>
<tr>
<th>Angiosperm</th>
<th>Dicotyledon</th>
<th>Photosynthesis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Assemblage</td>
<td>Domain</td>
<td>Phyla</td>
</tr>
<tr>
<td>Atmosphere</td>
<td>Ecosystem</td>
<td>Population</td>
</tr>
<tr>
<td>Autecology</td>
<td>Family</td>
<td>Primary productivity</td>
</tr>
<tr>
<td>Autotrophs</td>
<td>Food web</td>
<td>Respiration</td>
</tr>
<tr>
<td>Biomass</td>
<td>Genus, genera</td>
<td>Soil</td>
</tr>
<tr>
<td>Biome</td>
<td>Greenhouse effect</td>
<td>Species</td>
</tr>
<tr>
<td>Biosphere</td>
<td>Guild</td>
<td>Stomata</td>
</tr>
<tr>
<td>C3 Pathway</td>
<td>Gymnosperm</td>
<td>Synecology</td>
</tr>
<tr>
<td>C4 Pathway</td>
<td>Heterotrophs</td>
<td>Systematics</td>
</tr>
<tr>
<td>Chemosynthesis</td>
<td>Hydrosphere</td>
<td>Taxon, Taxa; Taxonomy</td>
</tr>
<tr>
<td>Class</td>
<td>Kingdom</td>
<td>Trophic level</td>
</tr>
<tr>
<td>Conifer</td>
<td>Metapopulations</td>
<td></td>
</tr>
<tr>
<td>Community</td>
<td>Monocotyledon</td>
<td></td>
</tr>
<tr>
<td>Crassulacean acid metabolism</td>
<td>Order</td>
<td></td>
</tr>
</tbody>
</table>

**(CAM) photosynthesis**

**REFERENCES AND FURTHER READING**

42 CHAPTER 2 SOME BASICS