52

An Introduction to Ecology and the Biosphere

▲ **Figure 52.1 What threatens this amphibian's survival?**

KEY CONCEPTS

52.1 Earth's climate varies by latitude and season and is changing rapidly

52.2 The structure and distribution of terrestrial biomes are controlled by climate and disturbance

52.3 Aquatic biomes are diverse and dynamic systems that cover most of Earth

52.4 Interactions between organisms and the environment limit the distribution of species

OVERVIEW

Discovering Ecology

When University of Delaware undergraduate Justin Yeager spent his summer abroad in Costa Rica, all he wanted was to see the tropical rain forest and to practice his Spanish. Instead, he rediscovered the variable harlequin toad (*Atelopus varius*), a species thought to be extinct in the mountain slopes of Costa Rica and Panama where it once lived **(Figure 52.1)**. During the 1980s and 1990s, roughly two-thirds of the 82 known species of harlequin toads vanished. Scientists think that a disease-causing chytrid fungus, *Batrachochytrium dendrobatidis* (see Figure 31.26), contributed to many of these extinctions. Why was the fungus suddenly thriving in the rain forest? Cloudier days and warmer nights associated with global warming appear to have created an environment ideal for its success. As of 2009, the species that Yeager found was surviving as a single known population of fewer than 100 individuals.

What environmental factors limit the geographic distribution of harlequin toads? How do variations in their food supply or interactions with other species, such as pathogens, affect the size of their population? Questions like these are the subject of **ecology** (from the Greek *oikos*, home, and *logos*, study), the scientific study of the interactions between organisms and the environment. Ecological interactions occur at a hierarchy of scales that ecologists study, from single organisms to the globe **(Figure 52.2)**.

Ecology's roots are in our basic human interest in observing other organisms. Naturalists, including Aristotle and Darwin, have long studied the living world and systematically recorded their observations. However, modern ecology involves more than observation. It is a rigorous experimental science that requires a breadth of biological knowledge. Ecologists generate hypotheses, manipulate environmental variables, and observe the outcome. In this unit, you will encounter many examples of ecological experiments, whose complex challenges have made ecologists innovators in experimental design and statistical inference.

In addition to providing a conceptual framework for understanding the field of ecology, Figure 52.2 provides the organizational framework for our final unit. In this chapter, we first describe Earth's climate and the importance of climate and other physical factors in determining the location of major life zones on land and in the oceans. We then examine how ecologists determine what controls the distribution and abundance of individual species. The next three chapters investigate population, community, and ecosystem ecology in detail, including approaches for restoring degraded ecosystems. The final chapter explores conservation biology and global ecology as we consider how ecologists apply biological knowledge to predict the global consequences of human activities and to conserve Earth's biodiversity.

CONCEPT 52.1

Earth's climate varies by latitude and season and is changing rapidly

The most significant influence on the distribution of organisms on land and in the oceans is **climate**, the long-term, prevailing weather conditions in a given area. Four physical

▼ **Figure 52.2**

Exploring The Scope of Ecological Research

Ecologists work at different levels of the biological hierarchy, from individual organisms to the planet. Here we present a sample research question for each level of the hierarchy.

Global Ecology

The **biosphere** is the global ecosystem—the sum of all the planet's ecosystems and landscapes. **Global ecology** examines how the regional exchange of energy and materials influences the functioning and distribution of organisms across the biosphere.

◀ How does ocean circulation affect the global distribution of crustaceans?

Landscape Ecology

A **landscape** (or seascape) is a mosaic of connected ecosystems. Research in **landscape ecology** focuses on the factors controlling exchanges of energy, materials, and organisms across multiple ecosystems.

◀ To what extent do the trees lining a river serve as corridors of dispersal for animals?

Ecosystem Ecology

An **ecosystem** is the community of organisms in an area and the physical factors with which those organisms interact. **Ecosystem ecology** emphasizes energy flow and chemical cycling between organisms and the environment.

◀ What factors control photosynthetic productivity in a temperate grassland ecosystem?

Community Ecology

A **community** is a group of populations of different species in an area. **Community ecology** examines how interactions between species, such as predation and competition, affect community structure and organization.

◀ What factors influence the diversity of species that make up a forest?

Population Ecology

A **population** is a group of individuals of the same species living in an area. **Population ecology** analyzes factors that affect population size and how and why it changes through time.

◀ What environmental factors affect the reproductive rate of locusts?

Organismal Ecology

Organismal ecology, which includes the subdisciplines of physiological, evolutionary, and behavioral ecology, is concerned with how an organism's structure, physiology, and behavior meet the challenges posed by its environment.

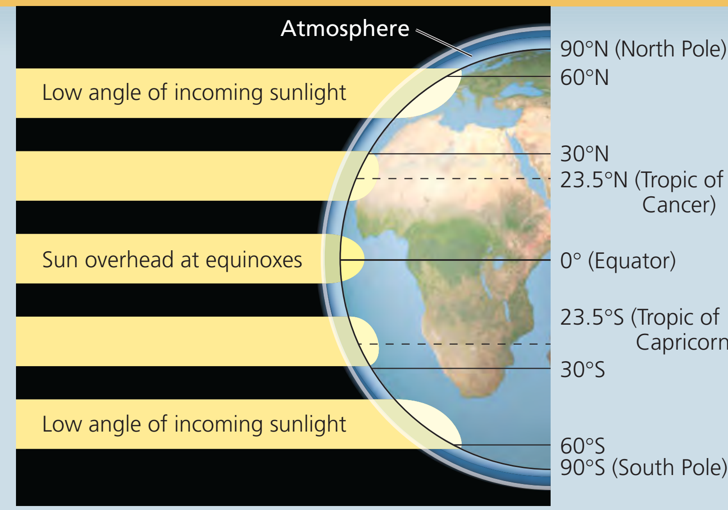
◀ How do hammerhead sharks select a mate?

▼ **Figure 52.3**

Exploring Global Climate Patterns

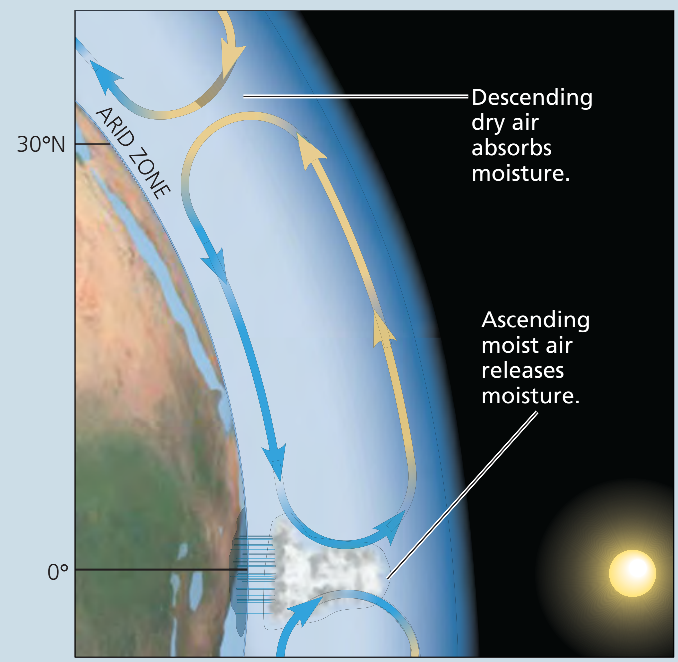
Latitudinal Variation in Sunlight Intensity

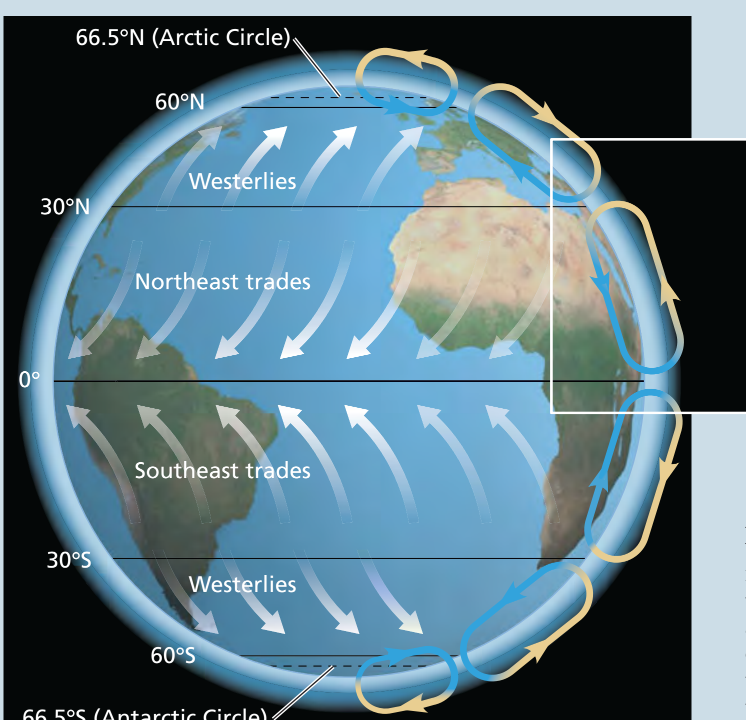
Earth's curved shape causes latitudinal variation in the intensity of sunlight. Because sunlight strikes the **tropics** (those regions that lie between 23.5° north latitude and 23.5° south latitude) most directly, more heat and light per unit of surface area are delivered there. At higher latitudes, sunlight strikes Earth at an oblique angle, and thus the light energy is more diffuse on Earth's surface.



Global Air Circulation and Precipitation Patterns

Intense solar radiation near the equator initiates a global pattern of air circulation and precipitation. High temperatures in the tropics evaporate water from Earth's surface and cause warm, wet air masses to rise (blue arrows) and flow toward the poles. The rising air masses release much of their water content, creating abundant precipitation in tropical regions. The high-altitude air masses, now dry, descend (tan arrows) toward Earth around 30° north and south, absorbing moisture from the land and creating an arid climate conducive to the development of the deserts that are common at those latitudes. Some of the descending air then flows toward the poles. At latitudes around 60° north and south, the air masses again rise and release abundant precipitation (though less than in the tropics). Some of the cold, dry rising air then flows to the poles, where it descends and flows back toward the equator, absorbing moisture and creating the comparatively rainless and bitterly cold climates of the polar regions.





Air flowing close to Earth's surface creates predictable global wind patterns. As Earth rotates on its axis, land near the equator moves faster than that at the poles, deflecting the winds from the vertical paths shown above and creating the more easterly and westerly flows shown at left. Cooling trade winds blow from east to west in the tropics; prevailing westerlies blow from west to east in the temperate zones, defined as the regions between the Tropic of Cancer and the Arctic Circle and between the Tropic of Capricorn and the Antarctic Circle.

factors—temperature, precipitation, sunlight, and wind—are particularly important components of climate. In this section, we will describe climate patterns at two scales: **macroclimate**, patterns on the global, regional, and landscape level; and **microclimate**, very fine, localized patterns, such as those encountered by the community of organisms that live in the microhabitat beneath a fallen log. First let's examine Earth's macroclimate.

Global Climate Patterns

Global climate patterns are determined largely by the input of solar energy and Earth's movement in space. The sun warms the atmosphere, land, and water. This warming establishes the temperature variations, cycles of air and water movement, and evaporation of water that cause dramatic latitudinal variations in climate. **Figure 52.3** summarizes Earth's climate patterns and how they are formed.

Regional and Local Effects on Climate

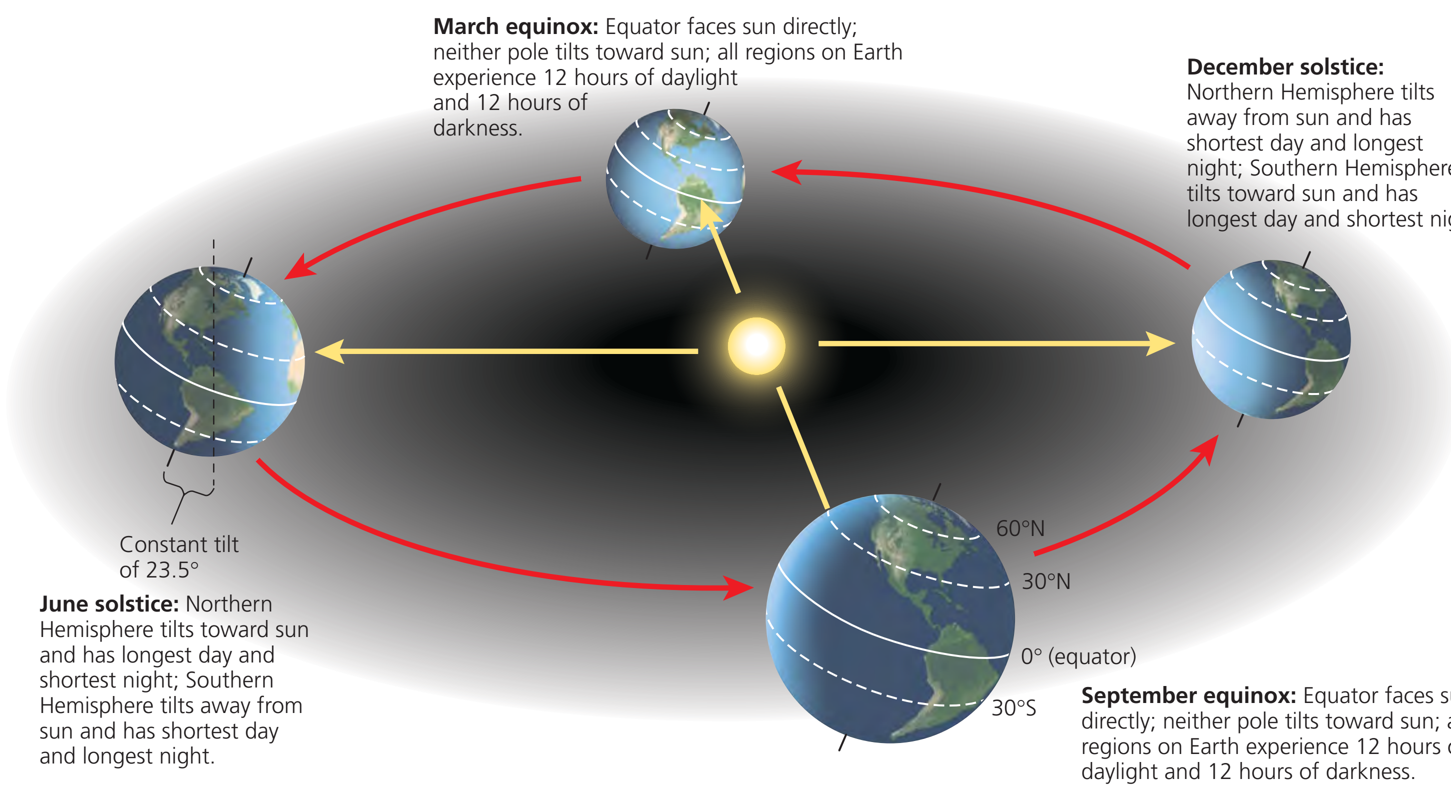
Climate patterns can be modified by many factors, including seasonal variation in climate, large bodies of water, and mountain ranges. We will examine each of these factors in more detail.

Seasonality

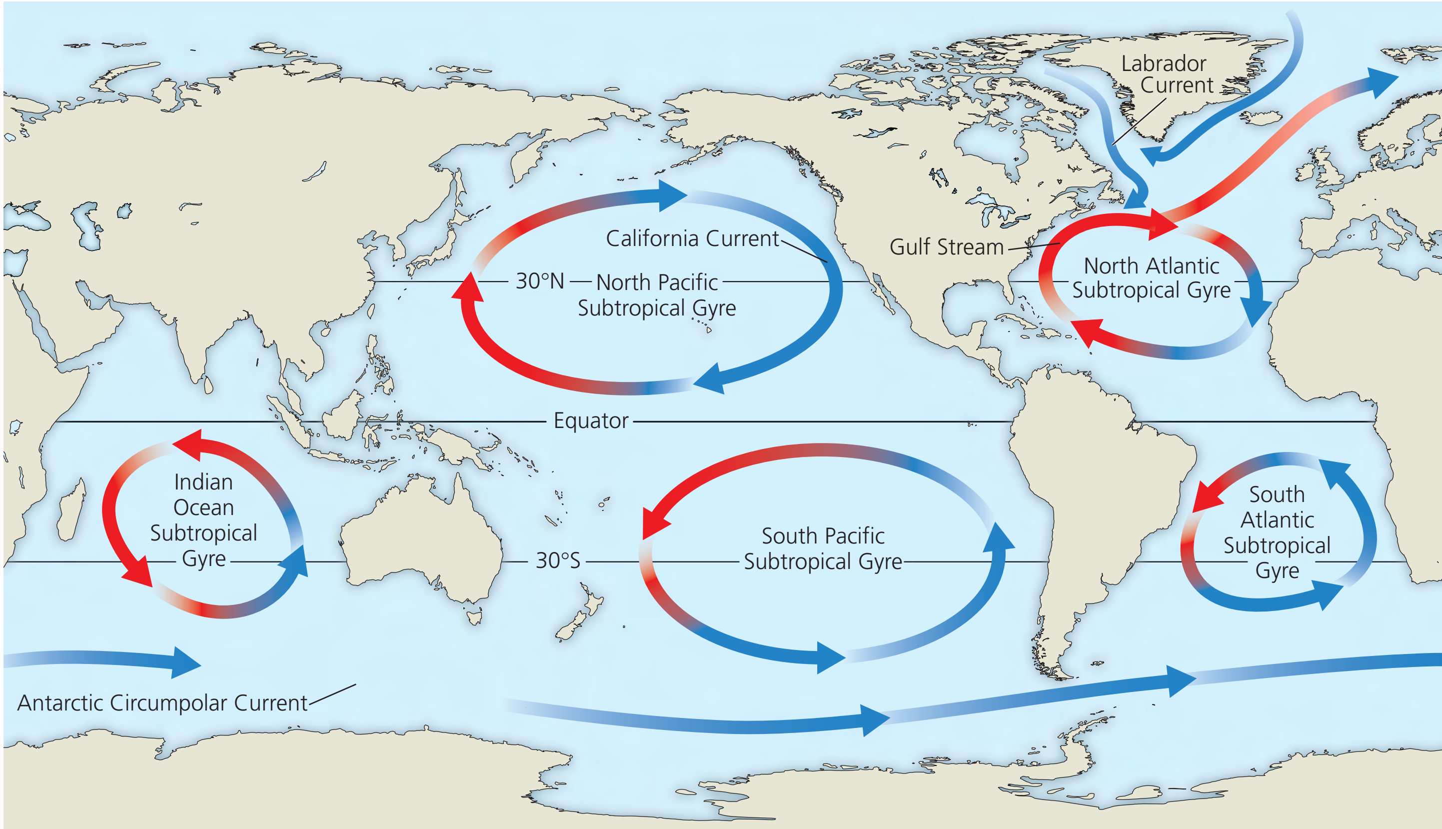
As described in **Figure 52.4**, Earth's tilted axis of rotation and its annual passage around the sun cause strong seasonal cycles in middle to high latitudes. In addition to these global changes in day length, solar radiation, and temperature, the changing angle of the sun over the course of the year affects local environments. For example, the belts of wet and dry air on either side of the equator move slightly northward and southward with the changing angle of the sun, producing marked wet and dry seasons around 20° north and 20° south latitude, where many tropical deciduous forests grow. In addition, seasonal changes in wind patterns alter ocean currents, sometimes causing the upwelling of cold water from deep ocean layers. This nutrient-rich water stimulates the growth of surface-dwelling phytoplankton and the organisms that feed on them.

Bodies of Water

Ocean currents influence climate along the coasts of continents by heating or cooling overlying air masses that pass across the land. Coastal regions are also generally wetter than inland areas at the same latitude. The cool, misty climate produced by the cold California Current that flows southward



▲ **Figure 52.4 Seasonal variation in sunlight intensity.** Because Earth is tilted on its axis relative to its plane of orbit around the sun, the intensity of solar radiation varies seasonally. This variation is smallest in the tropics and increases toward the poles.



▲ **Figure 52.5 Global circulation of surface water in the oceans.** Water is warmed at the equator and flows north and south toward the poles, where it cools. Note the similarities between the direction of water circulation in the gyres and the direction of the trade winds in Figure 52.3.

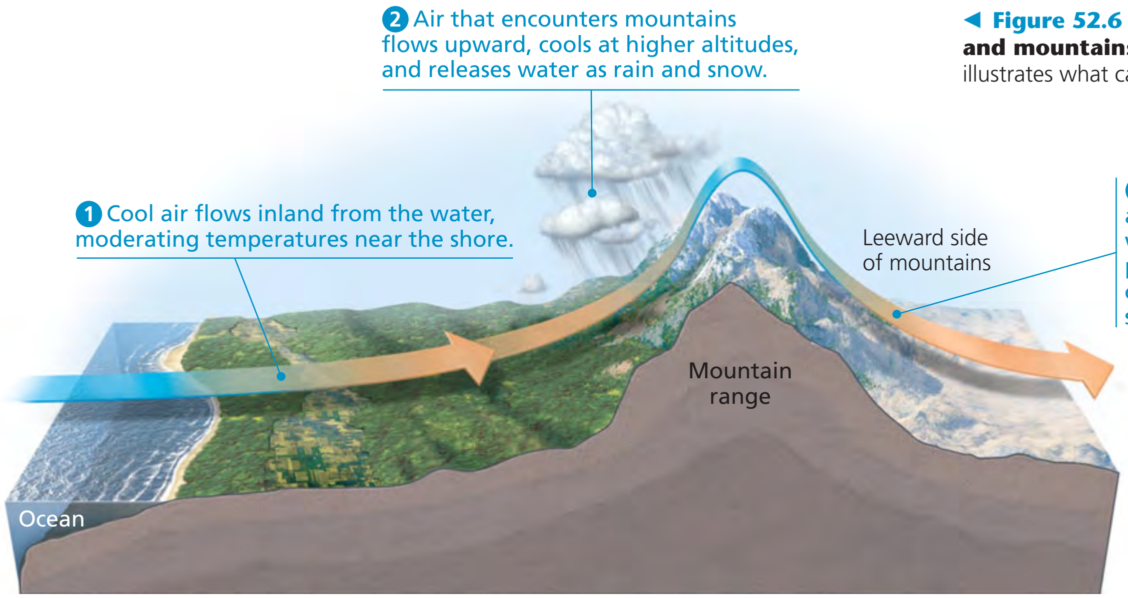
along western North America supports a coniferous rain forest ecosystem along much of the continent's Pacific coast and large redwood groves farther south. Conversely, the west coast of northern Europe has a mild climate because the Gulf Stream carries warm water from the equator to the North Atlantic **(Figure 52.5)**. As a result, northwestern Europe is warmer during winter than southeastern Canada, which is farther south but is cooled by the Labrador Current flowing south from the coast of Greenland.

Because of the high specific heat of water (see Chapter 3), oceans and large lakes tend to moderate the climate of nearby land. During a hot day, when land is warmer than the water, air over the land heats up and rises, drawing a cool breeze from the water across the land **(Figure 52.6)**. In contrast, because temperatures drop more quickly over land than over water at night, air over the now warmer water rises, drawing cooler air from the land back out over the water and replacing it with warmer air from offshore. This local moderation of climate can be limited to the coast itself, however. In regions such as southern California and southwestern Australia, cool, dry ocean breezes in summer are warmed when they contact the land, absorbing moisture and creating a hot, arid climate just a few kilometers inland (see Figure 3.5). This climate pattern also occurs around the Mediterranean Sea, which gives it the name *Mediterranean climate*.

Mountains

Like large bodies of water, mountains influence air flow over land. When warm, moist air approaches a mountain, the air rises and cools, releasing moisture on the windward side of the peak (see Figure 52.6). On the leeward side, cooler, dry air descends, absorbing moisture and producing a "rain shadow." This leeward rain shadow determines where many deserts are found, including the Great Basin and the Mojave Desert of western North America, the Gobi Desert of Asia, and the small deserts found in the southwest corners of some Caribbean islands.

Mountains also affect the amount of sunlight reaching an area and thus the local temperature and rainfall. South-facing slopes in the Northern Hemisphere receive more sunlight than north-facing slopes and are therefore warmer and drier. These physical differences influence species distributions locally. In many mountains of western North America, spruce and other conifers grow on the cooler north-facing slopes, but shrubby, drought-resistant plants inhabit the south-facing slopes. In addition, every 1,000-m increase in elevation



◀ **Figure 52.6 How large bodies of water and mountains affect climate.** This figure illustrates what can happen on a hot summer day.

produces an average temperature drop of approximately 6°C, equivalent to that produced by an 880-km increase in latitude. This is one reason that high-elevation communities at one latitude can be similar to those at lower elevations much farther from the equator.

Microclimate

Many features in the environment influence microclimate by casting shade, altering evaporation from soil, or changing wind patterns. Forest trees often moderate the microclimate below them. Cleared areas therefore typically experience greater temperature extremes than the forest interior because of greater solar radiation and wind currents that arise from the rapid heating and cooling of open land. Within a forest, low-lying ground is usually wetter than higher ground and tends to be occupied by different tree species. A log or large stone can shelter organisms such as salamanders, worms, and insects, buffering them from the extremes of temperature and moisture. Every environment on Earth is characterized by a mosaic of small-scale differences in **abiotic**, or nonliving, factors, the chemical and physical attributes, such as temperature, light, water, and nutrients, that influence the distribution and abundance of organisms. Later in this chapter, we will also examine how all of the **biotic**, or living, factors—the other organisms that are part of an individual's environment—similarly influence the distribution and abundance of life on Earth.

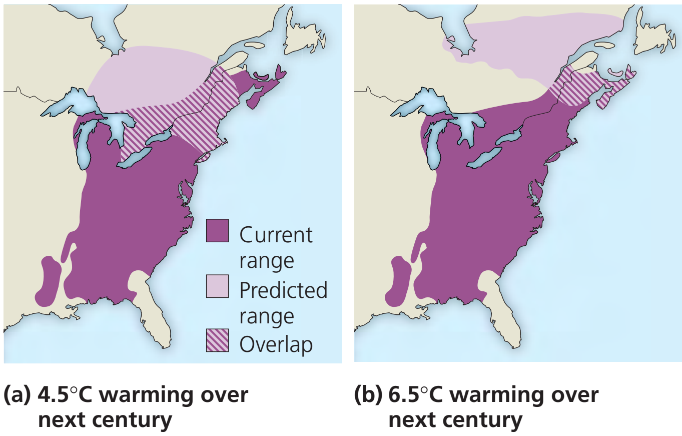
Global Climate Change

Because climatic variables affect the geographic ranges of most plants and animals, any large-scale change in Earth's climate profoundly affects the biosphere. In fact, such a large-scale climate "experiment" is already under way, a topic we will examine in more detail in Chapter 56. The burning of fossil fuels and deforestation are increasing the concentrations of carbon dioxide and other greenhouse gases in the atmosphere. As a result, Earth has warmed an average of 0.8°C (1.4°F) since 1900 and is projected to warm 1–6°C (2–11°F) more by the year 2100.

One way to predict the possible effects of future climate change on geographic ranges is to look back at the changes that have occurred in temperate regions since the last ice age ended. Until about 16,000 years ago, continental glaciers covered much of North America and Eurasia. As the climate warmed and the glaciers retreated, tree distributions expanded northward. A detailed record of these changes is captured in fossil pollen deposited in lakes and ponds. (Recall from Chapter 38 that wind and animals sometimes disperse pollen and seeds over great distances.) If researchers can determine the climatic limits of current distributions of organisms, they can make predictions about how those distributions may change with continued climatic warming.

A fundamental question when applying this approach to plants is whether seeds can disperse quickly enough to sustain the range shift of each species as climate changes. Fossil pollen shows that species with winged seeds that disperse relatively far from a parent tree, such as the sugar maple (*Acer saccharum*), expanded rapidly into the northeastern United States and Canada after the last ice age ended. In contrast, the northward range expansion of the eastern hemlock (*Tsuga canadensis*), whose seeds lack wings, was delayed nearly 2,500 years compared with the shift in suitable habitat.

Will plants and other species be able to keep up with the much more rapid warming projected for this century? Ecologists have attempted to answer this question for the American beech (*Fagus grandifolia*). Their models predict that the northern limit of the beech's range may move 700–900 km northward in the next century, and its southern range limit will

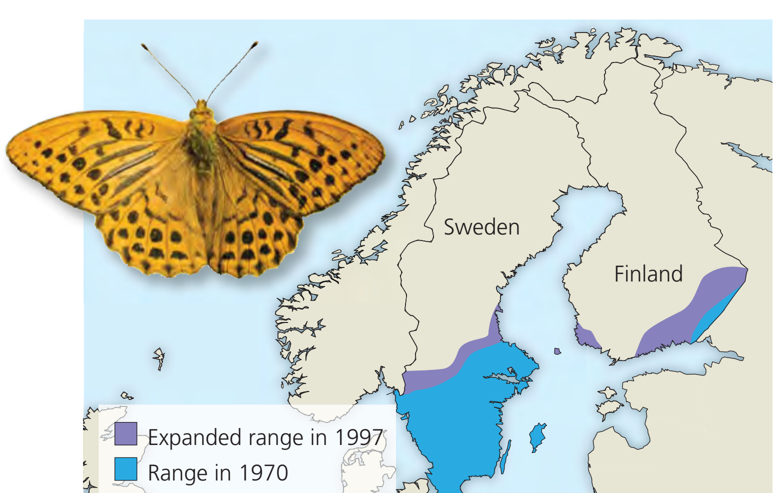


▲ **Figure 52.7 Current range and predicted range for the American beech under two climate-change scenarios.**

? *The predicted range in each scenario is based on climate factors alone. What other factors might alter the distribution of this species?*

shift even more. The current and predicted geographic ranges of this species under two different climate-change scenarios are illustrated in **Figure 52.7**. If these predictions are even approximately correct, the beech's range must shift 7–9 km northward per year to keep pace with the warming climate. However, since the end of the last ice age, the beech has moved at a rate of only 0.2 km per year. Without human help in moving to new habitats, species such as the American beech may have much smaller ranges or even become extinct.

Changes in the distributions of species are already evident in many well-studied groups of terrestrial, marine, and freshwater organisms, consistent with the signature of a warmer world. Ecologist Camille Parmesan (see interview on pp. 1142–1143) has studied range changes in European butterfly species, including the silver-washed fritillary (*Argynnis paphia*; see **Figure 52.8**). Parmesan and her colleagues found that the northern range limits of 22 of the 35 butterfly species studied had shifted farther north by 35–240 km over the time periods for which records exist, in some cases beginning in 1900. And other scientists have reported that a Pacific diatom species, *Neodenticula seminae*, recently has colonized the Atlantic Ocean for the first time in 800,000 years. As Arctic sea ice has receded in the past decade, the increased flow of water from the Pacific has swept these diatoms around Canada and into the Atlantic, where they quickly became established. The observation that many species are on the move in the face of climate change illustrates the importance of climate in determining species distributions, a topic we will explore further in the next section.



▲ **Figure 52.8 Northward range expansion of the silver-washed fritillary in Sweden and Finland.** This butterfly is one of many European species whose northern range limits have moved farther north in recent decades.

CONCEPT CHECK 52.1

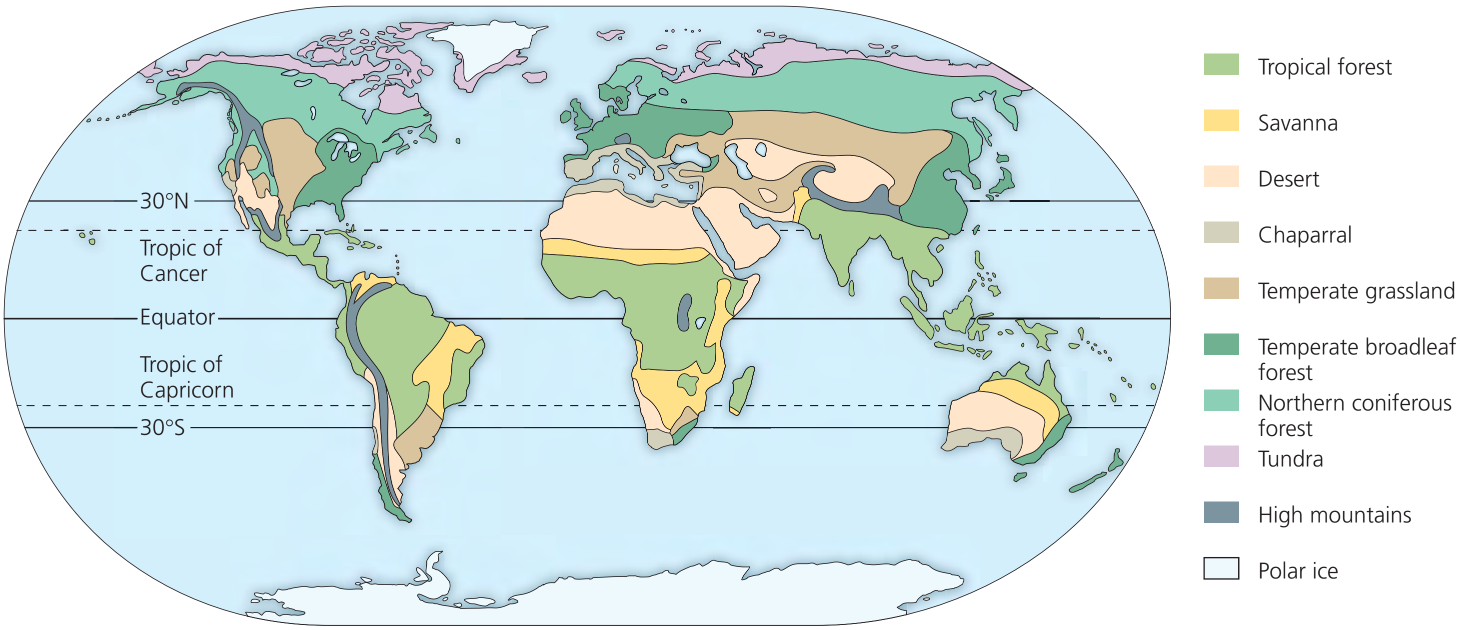
1. Explain how the sun's unequal heating of Earth's surface leads to the development of deserts around 30° north and south of the equator.
2. What are some of the differences in microclimate between an unplanted agricultural field and a nearby stream corridor with trees?
3. **WHAT IF?** Changes in Earth's climate at the end of the last ice age happened gradually, taking centuries to thousands of years. If the current global warming happens very quickly, as predicted, how may this rapid climate change affect the ability of long-lived trees to evolve, compared with annual plants, which have much shorter generation times?
4. **MAKE CONNECTIONS** In Concept 10.4 (pp. 199–201), you learned about the important differences between C_3 and C_4 plants. Focusing just on the effects of temperature, would you expect the global distribution of C_4 plants to expand or contract as Earth becomes warmer? Why?

For suggested answers, see Appendix A.

CONCEPT 52.2

The structure and distribution of terrestrial biomes are controlled by climate and disturbance

Throughout this book, you have seen many examples of how climate and other factors influence where individual species are found on Earth (see Figure 30.5, for instance). We turn now to the role of climate in determining the nature and location of Earth's **biomes**, major life zones characterized by vegetation type (in terrestrial biomes) or by the physical environment (in aquatic biomes). We first examine the influence of climate on terrestrial biomes, surveying aquatic systems later in the chapter.

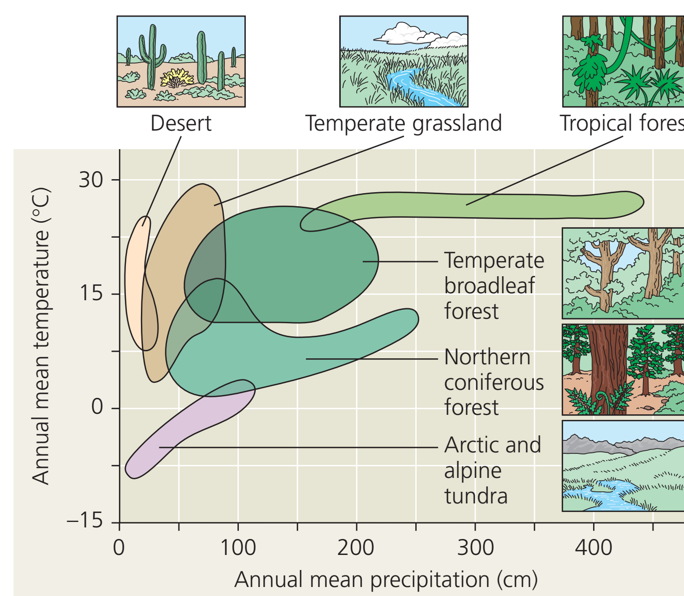


▲ **Figure 52.9 The distribution of major terrestrial biomes.** Although biomes are mapped here with sharp boundaries, biomes actually grade into one another, sometimes over large areas.

Climate and Terrestrial Biomes

Because of the latitudinal patterns of climate described in Figure 52.3, terrestrial biomes show strong latitudinal patterns in where they are found **(Figure 52.9)**. One way to highlight the importance of climate on the distribution of biomes is to construct a **climograph**, a plot of the annual mean temperature and precipitation in a particular region. **Figure 52.10** is a climograph for some of the biomes found in North America. Notice, for instance, that the range of precipitation in northern coniferous and temperate forests is similar but that temperate forests are generally warmer. Grasslands are typically drier than either kind of forest, and deserts are drier still.

Factors other than mean temperature and precipitation also play a role in determining where biomes exist. For example, some areas in North America with a particular combination of temperature and precipitation support a temperate broadleaf forest, but other areas with similar values for these variables support a coniferous forest (see the overlap in Figure 52.10). How might we explain this variation? First, remember that the climograph is based on annual *averages*. Often, however, the *pattern* of climatic variation is as important as the average climate. Some areas may receive regular precipitation throughout the year, whereas other areas may have distinct wet and dry seasons. A similar phenomenon may occur for temperature. In addition, other abiotic characteristics, such as the type of bedrock in an area, may greatly affect mineral nutrient availability and soil structure, which in turn affect the kind of vegetation that can grow.



▲ **Figure 52.10 A climograph for some major types of biomes in North America.** The areas plotted here encompass the ranges of annual mean temperature and precipitation in the biomes.

General Features of Terrestrial Biomes

Most terrestrial biomes are named for major physical or climatic features and for their predominant vegetation. Temperate grasslands, for instance, are generally found in middle latitudes, where the climate is more moderate than in the tropics or polar regions, and are dominated by various grass species (see Figure 52.9). Each biome is also characterized by microorganisms, fungi, and animals adapted to that particular environment. Temperate grasslands are usually more likely than temperate forests to be populated by large grazing mammals and to have arbuscular mycorrhizal fungi (see Figure 37.13).

Although Figure 52.9 shows distinct boundaries between the biomes, terrestrial biomes usually grade into each other without sharp boundaries. The area of intergradation, called an **ecotone**, may be wide or narrow.

Vertical layering is an important feature of terrestrial biomes, and the shapes and sizes of plants largely define that layering. In many forests, the layers from top to bottom consist of the upper **canopy**, the low-tree layer, the shrub understory, the ground layer of herbaceous plants, the forest floor (litter layer), and the root layer. Nonforest biomes have similar, though usually less pronounced, layers. Grasslands have an herbaceous layer of grasses and forbs (small broadleaf plants), a litter layer, and a root layer. Layering of vegetation provides many different habitats for animals, which sometimes exist in well-defined feeding groups, from the insectivorous birds and bats that feed above canopies to the small mammals, numerous worms, and arthropods that search for food in the litter and root layers below.

The species composition of each kind of biome varies from one location to another. For instance, in the northern coniferous forest (taiga) of North America, red spruce is common in the east but does not occur in most other areas, where black spruce and white spruce are abundant. As **Figure 52.11** shows, cacti living in deserts of North and South America appear very similar to plants called euphorbs found in African deserts. But since cacti and euphorbs belong to different evolutionary lineages, their similarities are due to convergent evolution (see Concept 22.3).

▲ ***Euphorbia canariensis***

◀ ***Cereus peruvianus***

▲ **Figure 52.11 Convergent evolution in a cactus and a euphorb.** *Cereus peruvianus*, a cactus, is found in the Americas; *Euphorbia canariensis*, a euphorb, is native to the Canary Islands, off the northwest coast of Africa.

Disturbance and Terrestrial Biomes

Biomes are dynamic, and disturbance rather than stability tends to be the rule. In ecological terms, **disturbance** is an event such as a storm, fire, or human activity that changes a community, removing organisms from it and altering resource availability. For instance, frequent fires can kill woody plants and keep a savanna from becoming the woodland that climate alone would support. Hurricanes and other storms create openings for new species in many tropical and temperate forests. Fires and outbreaks of pests, such as pine beetles and spruce budworms, produce gaps in northern coniferous forests that allow deciduous species, including aspen and birch, to grow. As a result of disturbances, biomes often exhibit extensive patchiness, with several different communities represented in a single area.

In many biomes, even the dominant plants depend on periodic disturbance. Natural wildfires are an integral component of grasslands, savannas, chaparral, and many coniferous forests. In North America, fires are no longer common across much of the Great Plains because tallgrass prairie ecosystems have been converted to agricultural fields that rarely burn. Before agricultural and urban development, much of the southeastern United States was dominated by a single conifer species, the longleaf pine. Without periodic burning, broadleaf trees tended to replace the pines. Forest managers now use fire as a tool to help maintain many coniferous forests.

Figure 52.12, on the next four pages, summarizes the major features of terrestrial biomes. As you read about the characteristics of each biome, remember that humans have altered much of Earth's surface, replacing natural communities with urban and agricultural ones. Most of the eastern United States, for example, is classified as temperate broadleaf forest, but little of that original forest remains.

CONCEPT CHECK 52.2

1. Based on the climograph in Figure 52.10, what mainly differentiates temperate grassland from temperate broadleaf forest?
2. Identify the natural biome in which you live, and summarize its abiotic and biotic characteristics. Do these reflect your actual surroundings? Explain.
3. **WHAT IF?** If global warming increases average temperatures on Earth by 4°C in this century, predict which biome is most likely to replace tundra in some locations as a result. Explain your answer.

For suggested answers, see Appendix A.

▼ **Figure 52.12**

Exploring Terrestrial Biomes

Tropical Forest

Distribution Equatorial and subequatorial regions

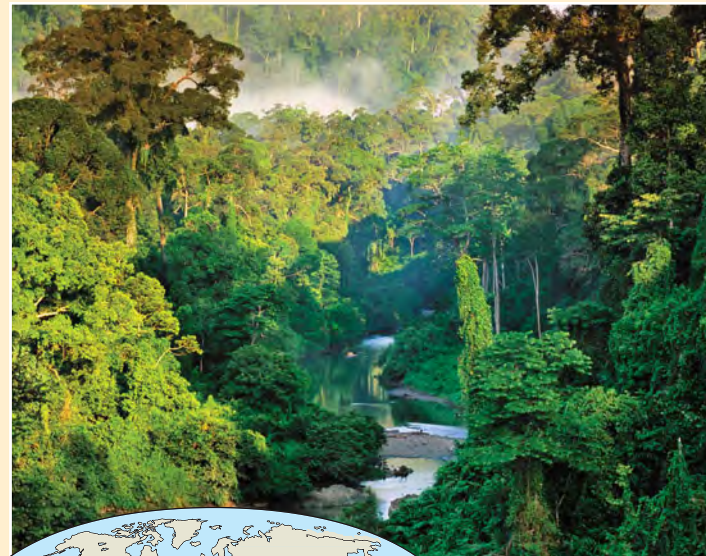
Precipitation In **tropical rain forests**, rainfall is relatively constant, about 200–400 cm annually. In **tropical dry forests**, precipitation is highly seasonal, about 150–200 cm annually, with a six- to seven-month dry season.

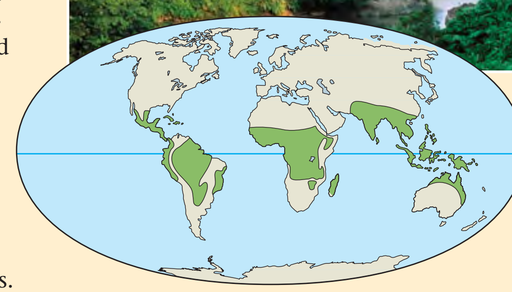
Temperature High year-round, averaging 25–29°C with little seasonal variation

Plants Tropical forests are vertically layered, and competition for light is intense. Layers in rain forests include emergent trees that grow above a closed canopy, the canopy trees, one or two layers of subcanopy trees, and layers of shrubs and herbs (small, nonwoody plants). There are generally fewer layers in tropical dry forests. Broadleaf evergreen trees are dominant in tropical rain forests, whereas many tropical dry forest trees drop their leaves during the dry season. Epiphytes such as bromeliads and orchids generally cover tropical forest trees but are less abundant in dry forests. Thorny shrubs and succulent plants are common in some tropical dry forests.

Animals Earth's tropical forests are home to millions of species, including an estimated 5–30 million still undescribed species of insects, spiders, and other arthropods. In fact, animal diversity is higher in tropical forests than in any other terrestrial biome. The animals, including amphibians, birds and other reptiles, mammals, and arthropods, are adapted to the vertically layered environment and are often inconspicuous.

Human Impact Humans long ago established thriving communities in tropical forests. Rapid population growth leading to agriculture and development is now destroying many tropical forests.

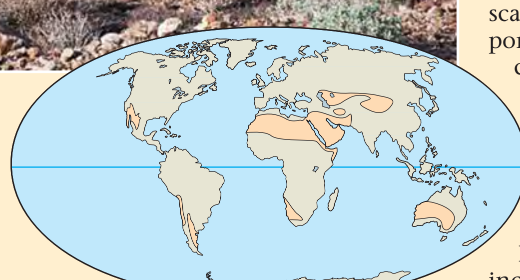




A tropical rain forest in Borneo

Desert

A desert in the southwestern United States



Distribution **Deserts** occur in bands near 30° north and south latitude or at other latitudes in the interior of continents (for instance, the Gobi Desert of north-central Asia).

Precipitation Precipitation is low and highly variable, generally less than 30 cm per year.

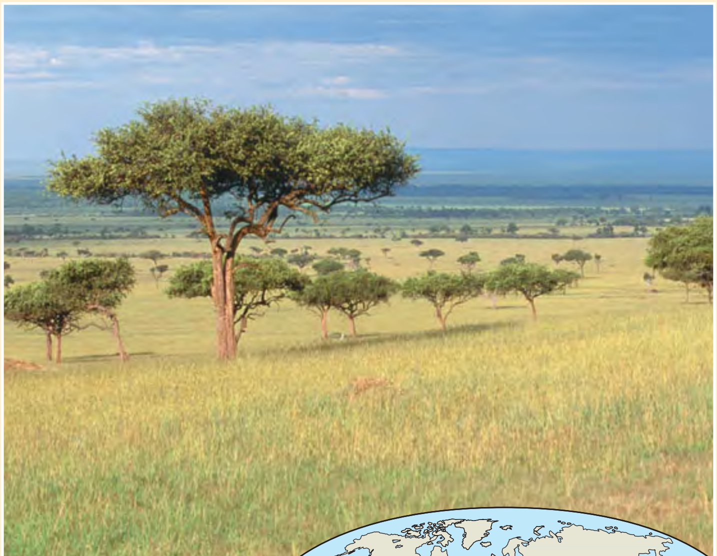
Temperature Temperature is variable seasonally and daily. Maximum air temperature in hot deserts may exceed 50°C; in cold deserts air temperature may fall below –30°C.

Plants Desert landscapes are dominated by low, widely scattered vegetation; the proportion of bare ground is high compared with other terrestrial biomes. The plants include succulents such as cacti or euphorbs, deeply rooted shrubs, and herbs that grow during the infrequent moist periods. Desert plant adaptations include heat and desiccation tolerance, water storage, and reduced leaf surface area. Physical defenses, such as spines, and chemical defenses, such as toxins in the leaves of shrubs, are common. Many of the plants exhibit C_4 or CAM photosynthesis (see Chapter 10).

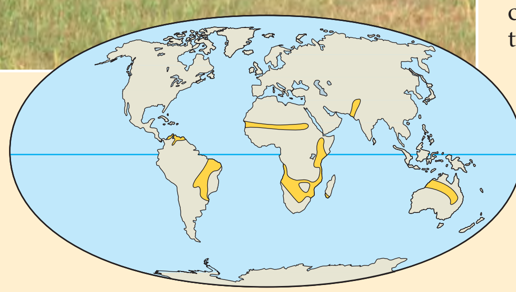
Animals Common desert animals include snakes and lizards, scorpions, ants, beetles, migratory and resident birds, and seed-eating rodents. Many species are nocturnal. Water conservation is a common adaptation, with some species surviving solely on water from breaking down carbohydrates in seeds.

Human Impact Long-distance transport of water and deep groundwater wells have allowed humans to maintain substantial populations in deserts. Urbanization and conversion to irrigated agriculture have reduced the natural biodiversity of some deserts.

Savanna



A savanna in Kenya



Distribution Equatorial and subequatorial regions

Precipitation Rainfall, which is seasonal, averages 30–50 cm per year. The dry season can last up to eight or nine months.

Temperature The **savanna** is warm year-round, averaging 24–29°C, but with somewhat more seasonal variation than in tropical forests.

Plants The scattered trees found at different densities in the savanna often are thorny and have small leaves, an apparent adaptation to the relatively dry conditions. Fires are common in the dry season, and the dominant plant species are fire-adapted and tolerant of seasonal drought. Grasses and small nonwoody plants called forbs, which make up most of the ground cover, grow rapidly in response to seasonal rains and are tolerant of grazing by large mammals and other herbivores.

Animals Large plant-eating mammals, such as wildebeests and zebras, and predators, including lions and hyenas, are common inhabitants. However, the dominant herbivores are actually insects, especially termites. During seasonal droughts, grazing mammals often migrate to parts of the savanna with more forage and scattered watering holes.

Human Impact There is evidence that the earliest humans lived in savannas. Fires set by humans may help maintain this biome, though overly frequent fires reduce tree regeneration by killing the seedlings and saplings. Cattle ranching and overhunting have led to declines in large-mammal populations.

Chaparral

Distribution This biome occurs in midlatitude coastal regions on several continents, and its many names reflect its far-flung distribution: **chaparral** in North America, *matorral* in Spain and Chile, *garigue* and *maquis* in southern France, and *fynbos* in South Africa.

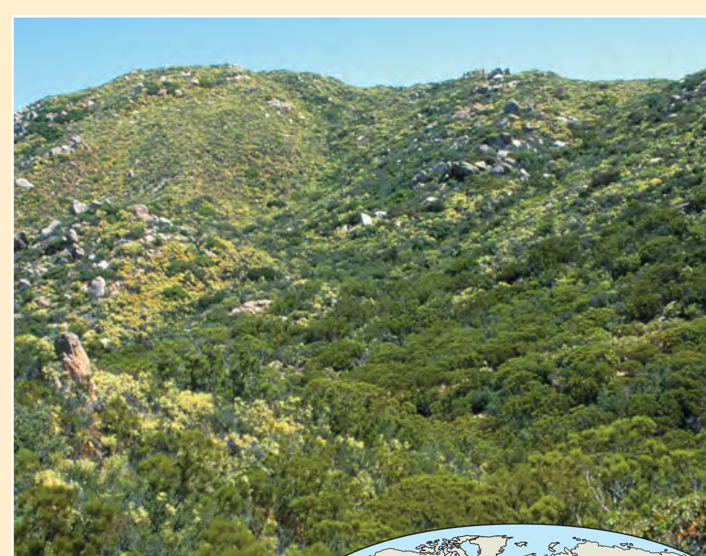
Precipitation Precipitation is highly seasonal, with rainy winters and dry summers. Annual precipitation generally falls within the range of 30–50 cm.

Temperature Fall, winter, and spring are cool, with average temperatures in the range of 10–12°C. Average summer temperature can reach 30°C, and daytime maximum temperature can exceed 40°C.

Plants Chaparral is dominated by shrubs and small trees, along with many kinds of grasses and herbs. Plant diversity is high, with many species confined to a specific, relatively small geographic area. Adaptations to drought include the tough evergreen leaves of woody plants, which reduce water loss. Adaptations to fire are also prominent. Some of the shrubs produce seeds that will germinate only after a hot fire; food reserves stored in their fire-resistant roots enable them to resprout quickly and use nutrients released by the fire.

Animals Native mammals include browsers, such as deer and goats, that feed on twigs and buds of woody vegetation, and a high diversity of small mammals. Chaparral areas also support many species of amphibians, birds and other reptiles, and insects.

Human Impact Chaparral areas have been heavily settled and reduced through conversion to agriculture and urbanization. Humans contribute to the fires that sweep across the chaparral.



An area of chaparral in California

Temperate Grassland

Distribution The veldts of South Africa, the *puszta* of Hungary, the pampas of Argentina and Uruguay, the steppes of Russia, and the plains and prairies of central North America are examples of **temperate grasslands**.

Precipitation Precipitation is often highly seasonal, with relatively dry winters and wet summers. Annual precipitation generally averages between 30 and 100 cm. Periodic drought is common.

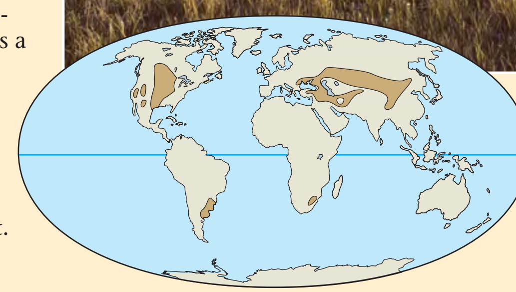
Temperature Winters are generally cold, with average temperatures frequently falling well below –10°C. Summers, with average temperatures often approaching 30°C, are hot.

Plants The dominant plants are grasses and forbs, which vary in height from a few centimeters to 2 m in tallgrass prairie. Many grassland plants have adaptations that help them survive periodic, protracted droughts and fire. For example, grasses can sprout quickly following fire. Grazing by large mammals helps prevent establishment of woody shrubs and trees.

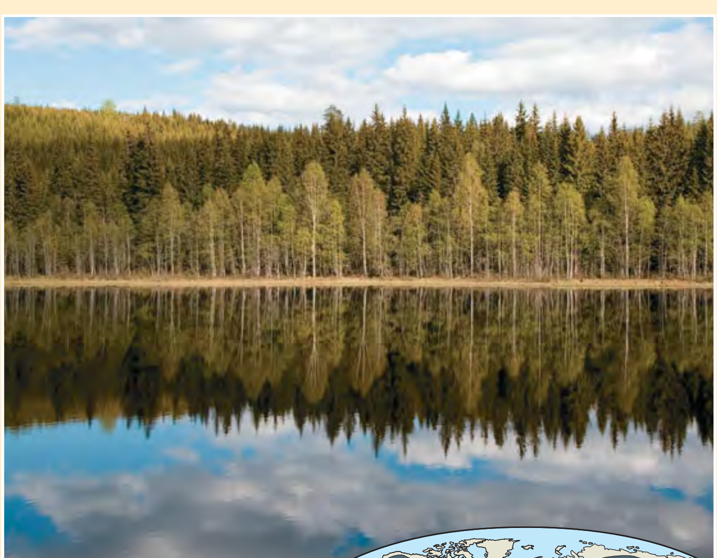
Animals Native mammals include large grazers such as bison and wild horses. Temperate grasslands are also inhabited by a wide variety of burrowing mammals, such as prairie dogs in North America.

Human Impact Deep, fertile soils make temperate grasslands ideal places for agriculture, especially for growing grains. As a consequence, most grassland in North America and much of Eurasia has been converted to farmland. In some drier grasslands, cattle and other grazers have turned parts of the biome into desert.

Grasslands National Park, Saskatchewan



Northern Coniferous Forest



A forest in Norway

Distribution Extending in a broad band across northern North America and Eurasia to the edge of the arctic tundra, the **northern coniferous forest**, or *taiga*, is the largest terrestrial biome on Earth.

Precipitation Annual precipitation generally ranges from 30 to 70 cm, and periodic droughts are common. However, some coastal coniferous forests of the U.S. Pacific Northwest are temperate rain forests that may receive over 300 cm of annual precipitation.

Temperature Winters are usually cold; summers may be hot. Some areas of coniferous forest in Siberia typically range in temperature from –50°C in winter to over 20°C in summer.

Plants Northern coniferous forests are dominated by cone-bearing trees, such as pine, spruce, fir, and hemlock, some of which depend on fire to regenerate. The conical shape of many conifers prevents too much snow from accumulating and breaking their branches, and their needle- or scale-like leaves reduce water loss. The diversity of plants in the shrub and herb layers of these forests is lower than in temperate broadleaf forests.

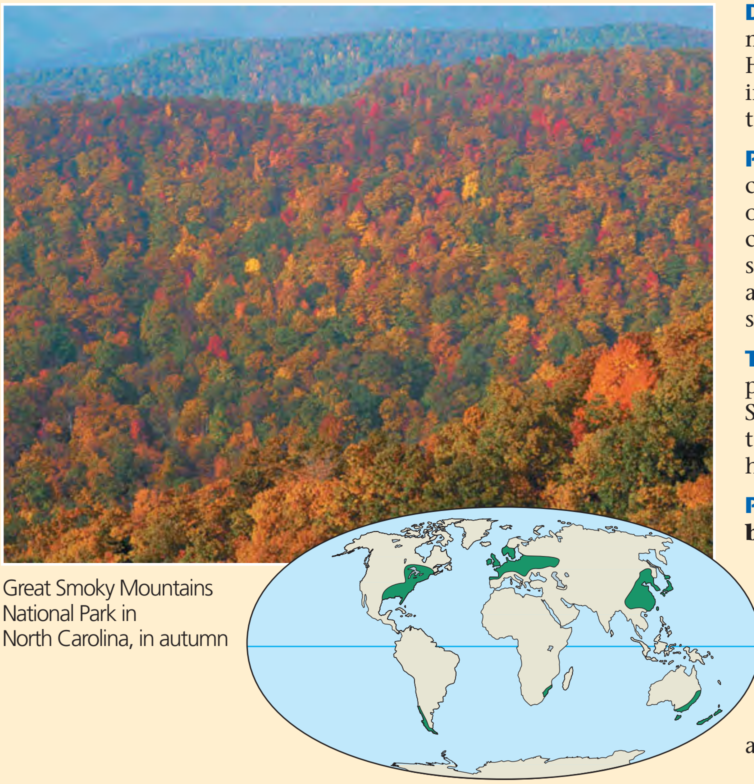
Animals While many migratory birds nest in northern coniferous forests, other species reside there year-round. The mammals of this biome, which include moose, brown bears, and Siberian tigers, are diverse. Periodic outbreaks of insects that feed on the dominant trees can kill vast tracts of trees.

Human Impact Although they have not been heavily settled by human populations, northern coniferous forests are being logged at an alarming rate, and the old-growth stands of these trees may soon disappear.

▼ **Figure 52.12 (continued)**

Exploring Terrestrial Biomes

Temperate Broadleaf Forest



Great Smoky Mountains National Park in North Carolina, in autumn

Distribution Found mainly at midlatitudes in the Northern Hemisphere, with smaller areas in Chile, South Africa, Australia, and New Zealand

Precipitation Precipitation can average from about 70 to over 200 cm annually. Significant amounts fall during all seasons, including summer rain and, in some forests, winter snow.

Temperature Winter temperatures average around 0°C. Summers, with maximum temperatures near 35°C, are hot and humid.

Plants A mature **temperate broadleaf forest** has distinct vertical layers, including a closed canopy, one or two strata of understory trees, a shrub layer, and an herb layer. There are few epiphytes. The dominant plants in the Northern Hemisphere are deciduous trees, which drop their leaves before winter, when low temperatures would reduce photosynthesis and make water uptake from frozen soil difficult. In Australia, evergreen eucalyptus trees dominate these forests.

Animals In the Northern Hemisphere, many mammals hibernate in winter, while many bird species migrate to warmer climates. Mammals, birds, and insects make use of all the vertical layers of the forest.

Human Impact Temperate broadleaf forest has been heavily settled on all continents. Logging and land clearing for agriculture and urban development have destroyed virtually all the original deciduous forests in North America. However, owing to their capacity for recovery, these forests are returning over much of their former range.

Tundra

Distribution **Tundra** covers expansive areas of the Arctic, amounting to 20% of Earth's land surface. High winds and low temperatures produce similar plant communities, called *alpine tundra*, on very high mountaintops at all latitudes, including the tropics.

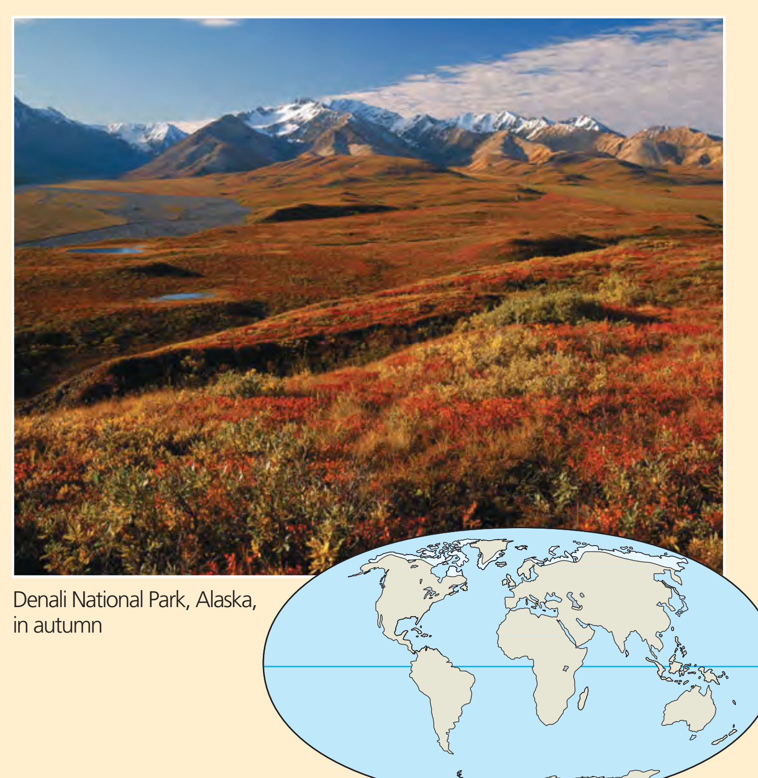
Precipitation Precipitation averages from 20 to 60 cm annually in arctic tundra but may exceed 100 cm in alpine tundra.

Temperature Winters are cold, with averages in some areas below –30°C. Summer temperatures generally average less than 10°C.

Plants The vegetation of tundra is mostly herbaceous, consisting of a mixture of mosses, grasses, and forbs, along with some dwarf shrubs and trees and lichens. A permanently frozen layer of soil called permafrost restricts the growth of plant roots.

Animals Large grazing musk oxen are resident, while caribou and reindeer are migratory. Predators include bears, wolves, and foxes. Many bird species migrate to the tundra for summer nesting.

Human Impact Tundra is sparsely settled but has become the focus of significant mineral and oil extraction in recent years.



Denali National Park, Alaska, in autumn

CONCEPT 52.3

Aquatic biomes are diverse and dynamic systems that cover most of Earth

Now that we have examined terrestrial biomes, let's turn to aquatic biomes. Unlike terrestrial biomes, aquatic biomes are characterized primarily by their physical environment. They also show far less latitudinal variation, with all types found across the globe. Ecologists distinguish between freshwater and marine biomes on the basis of physical and chemical differences. Marine biomes generally have salt concentrations that average 3%, whereas freshwater biomes are usually characterized by a salt concentration of less than 0.1%.

The oceans make up the largest marine biome, covering about 75% of Earth's surface. Because of their vast size, they greatly impact the biosphere. Water evaporated from the oceans provides most of the planet's rainfall, and ocean temperatures have a major effect on global climate and wind patterns (see Figure 52.3). Marine algae and photosynthetic bacteria also supply a substantial portion of the world's oxygen and consume large amounts of atmospheric carbon dioxide.

Freshwater biomes are closely linked to the soils and biotic components of the surrounding terrestrial biome. The particular characteristics of a freshwater biome are also influenced by the patterns and speed of water flow and the climate to which the biome is exposed.

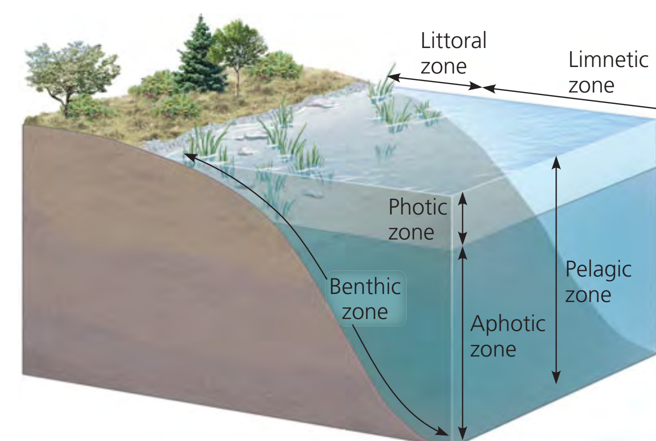
Zonation in Aquatic Biomes

Many aquatic biomes are physically and chemically stratified (layered), vertically and horizontally, as illustrated for both a lake and a marine environment in **Figure 52.13**. Light is absorbed by the water itself and by photosynthetic organisms, so its intensity decreases rapidly with depth. Ecologists distinguish between the upper **photic zone**, where there is sufficient light for photosynthesis, and the lower **aphotic zone**, where little light penetrates. The photic and aphotic zones together make up the **pelagic zone**. Deep in the aphotic zone lies the **abyssal zone**, the part of the ocean 2,000–6,000 m below the surface. At the bottom of all aquatic biomes, deep or shallow, is the **benthic zone**. Made up of sand and organic and inorganic sediments, the benthic zone is occupied by communities of organisms collectively called the **benthos**. A major source of food for many benthic species is dead organic matter called **detritus**, which "rains" down from the productive surface waters of the photic zone.

Thermal energy from sunlight warms surface waters to whatever depth the sunlight penetrates, but the deeper waters remain quite cold. In the ocean and in most lakes, a narrow layer of abrupt temperature change called a **thermocline**

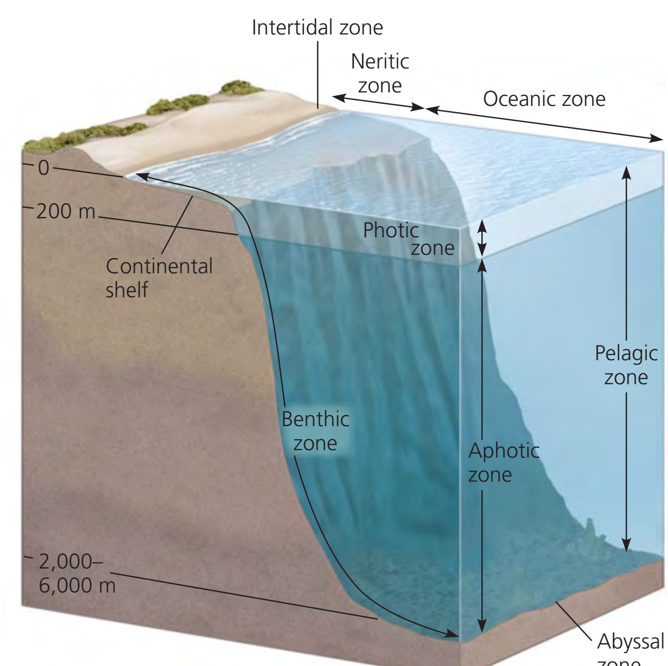
▼ **Figure 52.13 Zonation in aquatic environments.**

(a) Zonation in a lake



The lake environment is generally classified on the basis of three physical criteria: light penetration (photic and aphotic zones), distance from shore and water depth (littoral and limnetic zones), and whether the environment is open water (pelagic zone) or bottom (benthic zone).

(b) Marine zonation



Like lakes, the marine environment is generally classified on the basis of light penetration (photic and aphotic zones), distance from shore and water depth (intertidal, neritic, and oceanic zones), and whether the environment is open water (pelagic zone) or bottom (benthic and abyssal zones).

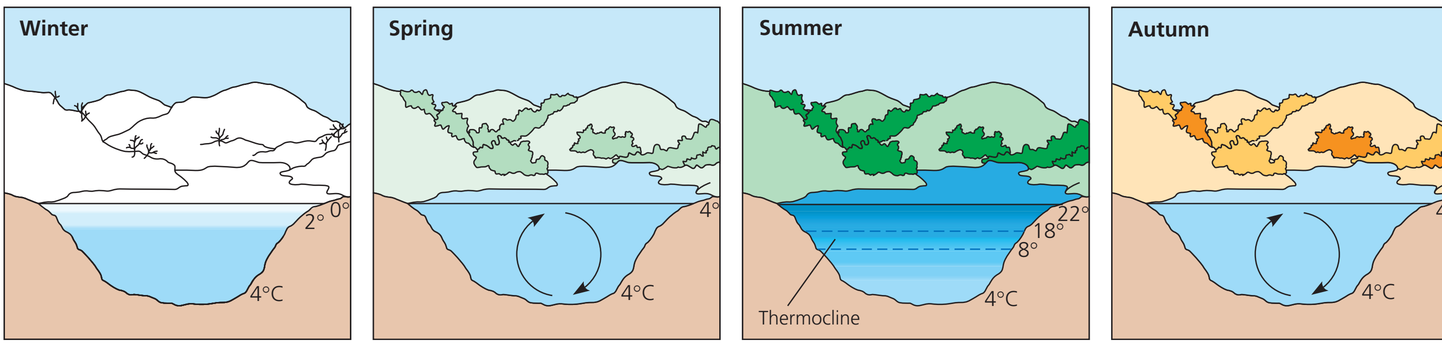
separates the more uniformly warm upper layer from more uniformly cold deeper waters. Lakes tend to be particularly layered with respect to temperature, especially during summer and winter, but many temperate lakes undergo a semiannual mixing of their waters as a result of changing temperature

1 In winter, the coldest water in the lake (0°C) lies just below the surface ice; water becomes progressively warmer at deeper levels of the lake, typically 4°C at the bottom.

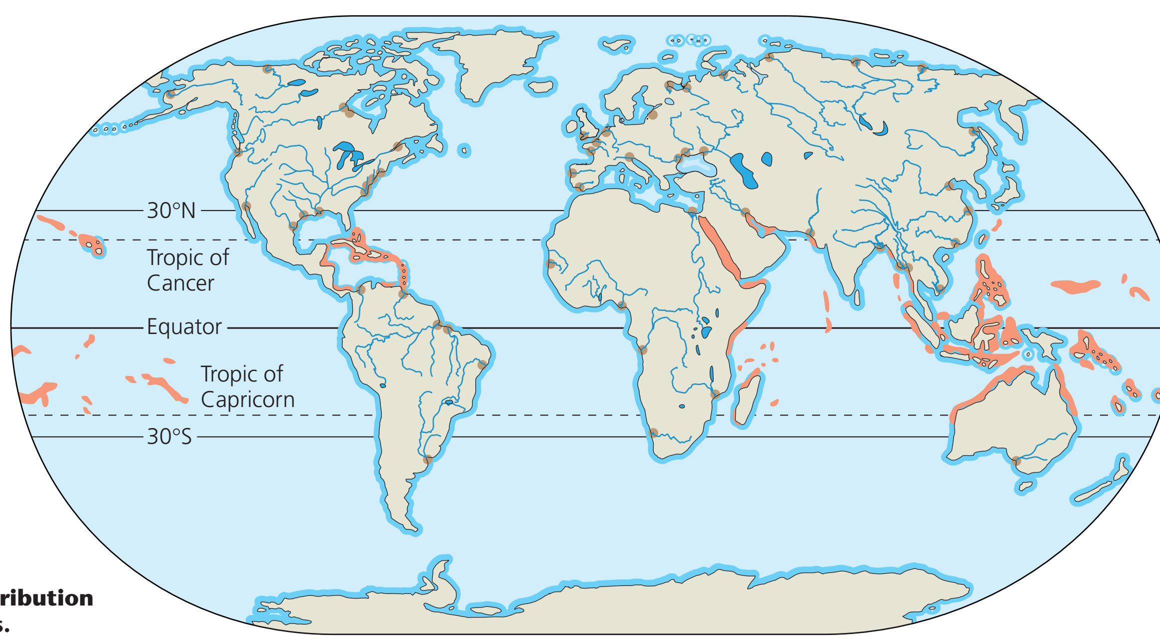
2 In spring, as the ice melts, the surface water warms to 4°C and mixes with the formerly cooler layers below, eliminating thermal stratification. Spring winds help mix the water, bringing oxygen to the bottom waters and nutrients to the surface.

3 In summer, the lake regains a distinctive thermal profile, with warm surface water separated from cold bottom water by a narrow vertical zone of abrupt temperature change, called a thermocline.

4 In autumn, as surface water cools rapidly, it sinks beneath the underlying layers, remixing the water until the surface begins to freeze and the winter temperature profile is reestablished.



▲ **Figure 52.14 Seasonal turnover in lakes with winter ice cover.** Because of the seasonal turnover shown here, lake waters are well oxygenated at all depths in spring and autumn; in winter and summer, when the lake is stratified by temperature, oxygen concentrations are lower in deeper waters and higher near the surface of the lake.



► **Figure 52.15 The distribution of major aquatic biomes.**

profiles **(Figure 52.14)**. This **turnover**, as it is called, sends oxygenated water from a lake's surface to the bottom and brings nutrient-rich water from the bottom to the surface in both spring and autumn. These cyclic changes in the abiotic properties of lakes are essential for the survival and growth of organisms at all levels within this ecosystem.

In both freshwater and marine environments, communities are distributed according to water depth, degree of light penetration, distance from shore, and whether they are found in open water or near the bottom. Marine communities, in particular, illustrate the limitations on species distribution that result from these abiotic factors. Plankton and many fish species occur in the relatively shallow photic zone (see Figure 52.13b). Because water absorbs light so well and the ocean is so deep, most of the ocean volume is virtually devoid of light (the aphotic zone) and harbors relatively little life, except for microorganisms and relatively sparse populations of fishes and invertebrates. Similar factors limit species distribution in deep lakes as well.

Figure 52.15 shows the locations of Earth's major aquatic biomes. **Figure 52.16**, on the next four pages, explores their main characteristics.

▼ **Figure 52.16**

Exploring Aquatic Biomes

Lakes

Physical Environment
Standing bodies of water range from ponds a few square meters in area to lakes covering thousands of square kilometers. Light decreases with depth, creating stratification (see Figure 52.13a). Temperate lakes may have a seasonal thermocline (see Figure 52.14); tropical lowland lakes have a thermocline year-round.

Chemical Environment The salinity, oxygen concentration, and nutrient content differ greatly among lakes and can vary with season. **Oligotrophic lakes** are nutrient-poor and generally oxygen-rich; **eutrophic lakes** are nutrient-rich and often depleted of oxygen in the deepest zone in summer and if covered with ice in winter. The amount of decomposable organic matter in bottom sediments is low in oligotrophic lakes and high in eutrophic lakes; high rates of decomposition in deeper layers of eutrophic lakes cause periodic oxygen depletion.

Geologic Features
Oligotrophic lakes may become more eutrophic over time as runoff adds sediments and nutrients. They tend to have less surface area relative to their depth than eutrophic lakes.

Photosynthetic Organisms Rooted and floating aquatic plants live in the **littoral zone**, the shallow, well-lit waters close to shore. Farther from shore, where water is too deep to support rooted aquatic plants, the **limnetic zone** is inhabited by a variety of phytoplankton, including cyanobacteria.

Heterotrophs In the limnetic zone, small drifting heterotrophs, or zooplankton, graze on the phytoplankton. The benthic zone is inhabited by assorted invertebrates whose species composition depends partly on oxygen levels. Fishes live in all zones with sufficient oxygen.

Human Impact Runoff from fertilized land and dumping of wastes lead to nutrient enrichment, which can produce algal blooms, oxygen depletion, and fish kills.


An oligotrophic lake in Grand Teton National Park, Wyoming


A eutrophic lake in the Okavango Delta, Botswana

Wetlands

Physical Environment A **wetland** is a habitat that is inundated by water at least some of the time and that supports plants adapted to water-saturated soil. Some wetlands are inundated at all times, whereas others flood infrequently.

Chemical Environment
Because of high organic production by plants and decomposition by microbes and other organisms, both the water and the soils are periodically low in dissolved oxygen. Wetlands have a high capacity to filter dissolved nutrients and chemical pollutants.


A basin wetland in the United Kingdom

Geologic Features *Basin wetlands* develop in shallow basins, ranging from upland depressions to filled-in lakes and ponds. *Riverine wetlands* develop along shallow and periodically flooded banks of rivers and streams. *Fringe wetlands* occur along the coasts of large lakes and seas, where water flows back and forth because of rising lake levels or tidal action. Thus, fringe wetlands include both freshwater and marine biomes.

Photosynthetic Organisms
Wetlands are among the most productive biomes on Earth. Their water-saturated soils favor the growth of plants such as floating pond lilies and emergent cattails, many sedges, tamarack, and black spruce, which have adaptations enabling them to grow in water or in soil that is periodically anaerobic owing to the presence of unaerated water. Woody plants dominate the vegetation of swamps, while bogs are dominated by sphagnum mosses.

Heterotrophs Wetlands are home to a diverse community of invertebrates, birds, and many other organisms. Herbivores, from crustaceans and aquatic insect larvae to muskrats, consume algae, detritus, and plants. Carnivores are also varied and may include dragonflies, otters, frogs, alligators, and herons.

Human Impact Draining and filling have destroyed up to 90% of wetlands, which help purify water and reduce peak flooding.

▼ **Figure 52.16 (continued)**

Exploring Aquatic Biomes

Streams and Rivers

Physical Environment The most prominent physical characteristic of streams and rivers is their current. Headwater streams are generally cold, clear, turbulent, and swift. Farther downstream, where numerous tributaries may have joined, forming a river, the water is generally warmer and more turbid because of suspended sediment. Streams and rivers are stratified into vertical zones.

Chemical Environment The salt and nutrient content of streams and rivers increases from the headwaters to the mouth. Headwaters are generally rich in oxygen. Downstream water may also contain substantial oxygen, except where there has been organic enrichment. A large fraction of the organic matter in rivers consists of dissolved or highly fragmented material that is carried by the current from forested streams.

Geologic Features Headwater stream channels are often narrow, have a rocky bottom, and alternate between shallow sections and deeper pools. The downstream stretches of rivers are generally wide and meandering. River bottoms are often silty from sediments deposited over long periods of time.

Photosynthetic Organisms Headwater streams that flow through grasslands or deserts may be rich in phytoplankton or rooted aquatic plants.

Heterotrophs A great diversity of fishes and invertebrates inhabit unpolluted rivers and streams, distributed according to, and throughout, the vertical zones. In streams flowing through temperate or tropical forests, organic matter from terrestrial vegetation is the primary source of food for aquatic consumers.

Human Impact Municipal, agricultural, and industrial pollution degrade water quality and kill aquatic organisms. Damming and flood control impair the natural functioning of stream and river ecosystems and threaten migratory species such as salmon.

A headwater stream in the Great Smoky Mountains

The Loire River (in France) far from its headwaters

Estuaries

An estuary in the southeastern United States

Physical Environment An **estuary** is a transition area between river and sea. Seawater flows up the estuary channel during a rising tide and flows back down during the falling tide. Often, higher-density seawater occupies the bottom of the channel and mixes little with the lower-density river water at the surface.

Chemical Environment Salinity varies spatially within estuaries, from nearly that of fresh water to that of seawater. Salinity also varies with the rise and fall of the tides. Nutrients from the river make estuaries, like wetlands, among the most productive biomes.

Geologic Features Estuarine flow patterns combined with the sediments carried by river and tidal waters create a complex network of tidal channels, islands, natural levees, and mudflats.

Photosynthetic Organisms Saltmarsh grasses and algae, including phytoplankton, are the major producers in estuaries.

Heterotrophs Estuaries support an abundance of worms, oysters, crabs, and many fish species that humans consume. Many marine invertebrates and fishes use estuaries as a breeding ground or migrate through them to freshwater habitats upstream. Estuaries are also crucial feeding areas for waterfowl and some marine mammals.

Human Impact Filling, dredging, and pollution from upstream have disrupted estuaries worldwide.

Intertidal Zones

Physical Environment An **intertidal zone** is periodically submerged and exposed by the tides, twice daily on most marine shores. Upper zones experience longer exposures to air and greater variations in temperature and salinity. Changes in physical conditions from the upper to the lower intertidal zones limit the distributions of many organisms to particular strata, as shown in the photograph.

Rocky intertidal zone on the Oregon coast

Chemical Environment Oxygen and nutrient levels are generally high and are renewed with each turn of the tides.

Geologic Features The substrates of intertidal zones, which are generally either rocky or sandy, select for particular behavior and anatomy among intertidal organisms. The configuration of bays or coastlines influences the magnitude of tides and the relative exposure of intertidal organisms to wave action.

Photosynthetic Organisms A high diversity and biomass of attached marine algae inhabit rocky intertidal zones, especially in the lower zone. Sandy intertidal zones exposed to vigorous wave action generally lack attached plants or algae, while sandy intertidal zones in protected bays or lagoons often support rich beds of seagrass and algae.

Heterotrophs Many of the animals in rocky intertidal environments have structural adaptations that enable them to attach to the hard substrate. The composition, density, and diversity of animals change markedly from the upper to the lower intertidal zones. Many of the animals in sandy or muddy intertidal zones, such as worms, clams, and predatory crustaceans, bury themselves and feed as the tides bring sources of food. Other common animals are sponges, sea anemones, echinoderms, and small fishes.

Human Impact Oil pollution has disrupted many intertidal areas. The construction of rock walls and barriers to reduce erosion from waves and storm surges has disrupted this zone in some locations.

Oceanic Pelagic Zone

Physical Environment The **oceanic pelagic zone** is a vast realm of open blue water, constantly mixed by wind-driven oceanic currents. Because of higher water clarity, the photic zone extends to greater depths than in coastal marine waters.

Chemical Environment Oxygen levels are generally high. Nutrient concentrations are generally lower than in coastal waters. Because they are thermally stratified year-round, some tropical areas of the oceanic pelagic zone have lower nutrient concentrations than temperate oceans. Turnover between fall and spring renews nutrients in the photic zones of temperate and high-latitude ocean areas.

Open ocean off the island of Hawaii

Geologic Features This biome covers approximately 70% of Earth's surface and has an average depth of nearly 4,000 m. The deepest point in the ocean is more than 10,000 m beneath the surface.

Photosynthetic Organisms The dominant photosynthetic organisms are phytoplankton, including photosynthetic bacteria, that drift with the oceanic currents. Spring turnover renews nutrients in temperate oceans producing a surge of phytoplankton growth. Because of the large extent of this biome, photosynthetic plankton account for about half of the photosynthetic activity on Earth.

Heterotrophs The most abundant heterotrophs in this biome are zooplankton. These protists, worms, copepods, shrimp-like krill, jellies, and small larvae of invertebrates and fishes graze on photosynthetic plankton. The oceanic pelagic zone also includes free-swimming animals, such as large squids, fishes, sea turtles, and marine mammals.

Human Impact Overfishing has depleted fish stocks in all Earth's oceans, which have also been polluted by waste dumping.

▼ **Figure 52.16 (continued)**

Exploring Aquatic Biomes

Coral Reefs

Physical Environment **Coral reefs** are formed largely from the calcium carbonate skeletons of corals. Shallow reef-building corals live in the photic zone of relatively stable tropical marine environments with high water clarity, primarily on islands and along the edge of some continents. They are sensitive to temperatures below about 18–20°C and above 30°C. Deep-sea coral reefs, found between 200 and 1,500 m deep, are less known than their shallow counterparts but harbor as much diversity as many shallow reefs do.

Chemical Environment Corals require high oxygen levels and are excluded by high inputs of fresh water and nutrients.

Geologic Features Corals require a solid substrate for attachment. A typical coral reef begins as a *fringing reef* on a young, high island, forming an offshore *barrier reef* later in the history of the island and becoming a *coral atoll* as the older island submerges.

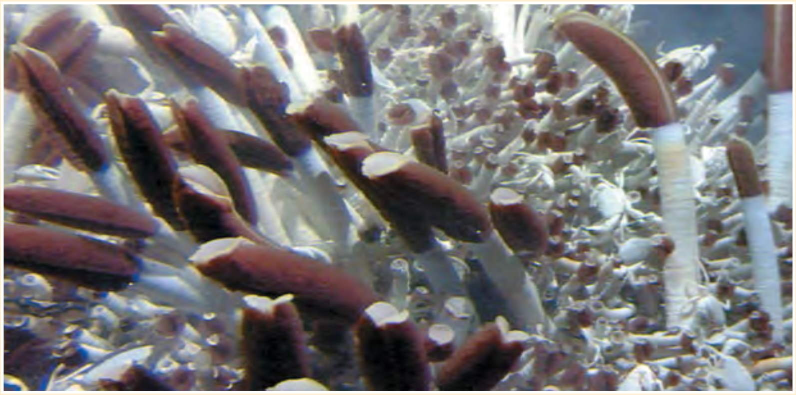
Photosynthetic Organisms Unicellular algae live within the tissues of the corals, forming a mutualistic relationship that provides the corals with organic molecules. Diverse multicellular red and green algae growing on the reef also contribute substantial amounts of photosynthesis.

Heterotrophs Corals, a diverse group of cnidarians (see Chapter 33), are themselves the predominant animals on coral reefs. However, fish and invertebrate diversity is exceptionally high. Overall animal diversity on coral reefs rivals that of tropical forests.

Human Impact Collecting of coral skeletons and overfishing have reduced populations of corals and reef fishes. Global warming and pollution may be contributing to large-scale coral death. Development of coastal mangroves for aquaculture has also reduced spawning grounds for many species of reef fishes.

A coral reef in the Red Sea

Marine Benthic Zone



A deep-sea hydrothermal vent community

Physical Environment The **marine benthic zone** consists of the seafloor below the surface waters of the coastal, or **neritic**, zone and the offshore, pelagic zone (see Figure 52.13b). Except for shallow, near-coastal areas, the marine benthic zone receives no sunlight. Water temperature declines with depth, while pressure increases. As a result, organisms in the very deep benthic, or abyssal, zone are adapted to continuous cold (about 3°C) and very high water pressure.

Chemical Environment Except in areas of organic enrichment, oxygen is usually present at sufficient concentrations to support diverse animal life.

Geologic Features Soft sediments cover most of the benthic zone. However, there are areas of rocky substrate on reefs, submarine mountains, and new oceanic crust.

Autotrophs Photosynthetic organisms, mainly seaweeds and filamentous algae, are limited to shallow benthic areas with sufficient light to support them. Unique assemblages of organisms, such as those shown in the photo, are found near **deep-sea hydrothermal vents** on mid-ocean ridges. In these dark, hot environments, the food producers are chemoautotrophic prokaryotes (see Chapter 27) that obtain energy by oxidizing H_2S formed by a reaction of the hot water with dissolved sulfate (SO_4^{2-}).

Heterotrophs Neritic benthic communities include numerous invertebrates and fishes. Beyond the photic zone, most consumers depend entirely on organic matter raining down from above. Among the animals of the deep-sea hydrothermal vent communities are giant tube worms (pictured at left), some more than 1 m long. They are nourished by chemoautotrophic prokaryotes that live as symbionts within their bodies. Many other invertebrates, including arthropods and echinoderms, are also abundant around the hydrothermal vents.

Human Impact Overfishing has decimated important benthic fish populations, such as the cod of the Grand Banks off Newfoundland. Dumping of organic wastes has created oxygen-deprived benthic areas.

CONCEPT CHECK 52.3

The first two questions refer to Figure 52.16.

1. Why are phytoplankton, and not benthic algae or rooted aquatic plants, the dominant photosynthetic organisms of the oceanic pelagic zone?
2. **MAKE CONNECTIONS** Many organisms living in estuaries experience freshwater and saltwater conditions each day with the rising and falling of tides. Based on what you learned in Concept 44.1 (pp. 953–958), explain how these changing conditions challenge the survival of these organisms.
3. **WHAT IF?** Water leaving a reservoir behind a dam is often taken from deep layers of the reservoir. Would you expect fish found in a river below a dam in summer to be species that prefer colder or warmer water than fish found in an undammed river? Explain.

For suggested answers, see Appendix A.

CONCEPT 52.4

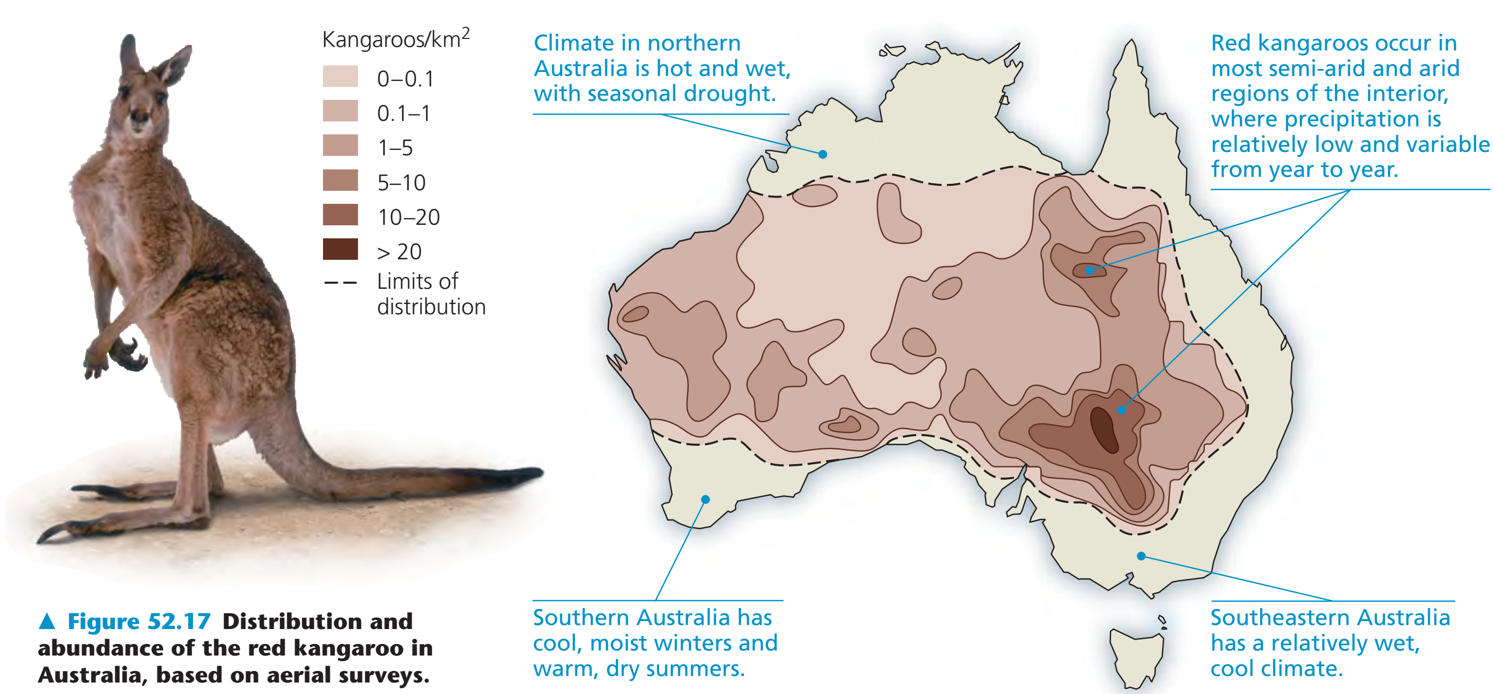
Interactions between organisms and the environment limit the distribution of species

So far in this chapter we've examined Earth's climate and the characteristics of terrestrial and aquatic biomes. We've also introduced the range of biological levels at which ecologists work (see Figure 52.2). In this section, we will examine how ecologists determine what factors control the distribution of species, such as the harlequin toad shown in Figure 52.1.

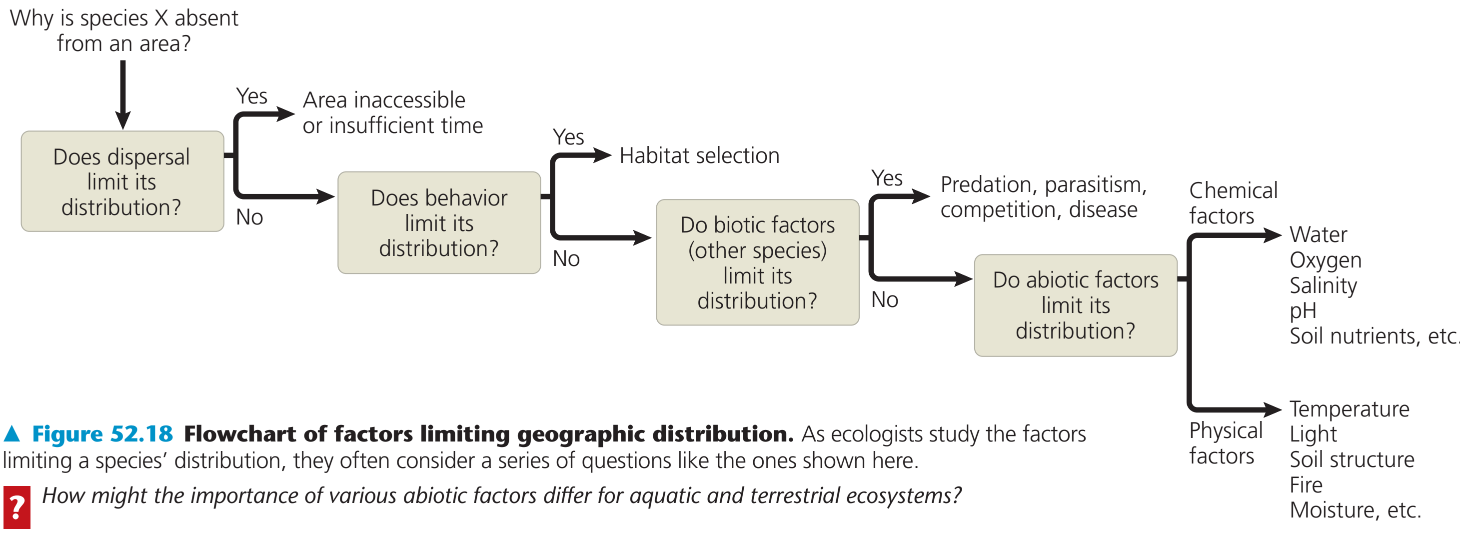
Species distributions are a consequence of both ecological and evolutionary interactions through time. The differential survival and reproduction of individuals that lead to evolution occur in *ecological time*, the minute-to-minute time frame of interactions between organisms and the environment. Through natural selection, organisms adapt to their environment over the time frame of many generations, in *evolutionary time*. One example of how events in ecological time have led to evolution is the selection for beak depth in Galápagos finches (see Figures 23.1 and 23.2). On the island of Daphne Major, finches with larger, deeper beaks were better able to survive during a drought because they could eat the large, hard seeds that were available. Finches with shallower beaks, which required smaller, softer seeds that were in short supply, were less likely to survive and reproduce. Because beak depth is hereditary in this species, the generation of finches born after the drought had beaks that were deeper than those of previous generations.

Biologists have long recognized global and regional patterns in the distribution of organisms (see the discussion of biogeography in Chapter 22). Kangaroos, for instance, are found in Australia but nowhere else on Earth. Ecologists ask not only *where* species occur, but also *why* species occur where they do: What factors determine their distribution? In seeking to answer this question, ecologists focus on both biotic and abiotic factors that influence the distribution and abundance of organisms.

Figure 52.17 presents an example of how both kinds of factors might affect the distribution of a species, in this case the red kangaroo (*Macropus rufus*). As the figure shows, red kangaroos are most abundant in a few areas in the interior of Australia, where precipitation is relatively sparse and variable. They are not found around most of the periphery of the continent,



▲ **Figure 52.17 Distribution and abundance of the red kangaroo in Australia, based on aerial surveys.**



▲ **Figure 52.18 Flowchart of factors limiting geographic distribution.** As ecologists study the factors limiting a species' distribution, they often consider a series of questions like the ones shown here.

? *How might the importance of various abiotic factors differ for aquatic and terrestrial ecosystems?*

where the climate is wetter. At first glance, this distribution might suggest that an abiotic factor—the amount and variability of precipitation—directly determines where red kangaroos live. However, climate may also influence red kangaroo populations indirectly through biotic factors, such as pathogens, parasites, predators, competitors, and food availability. Ecologists generally need to consider multiple factors and alternative hypotheses when attempting to explain the distribution of species.

To see how ecologists might arrive at such an explanation, let's work our way through the series of questions in the flowchart in **Figure 52.18.**

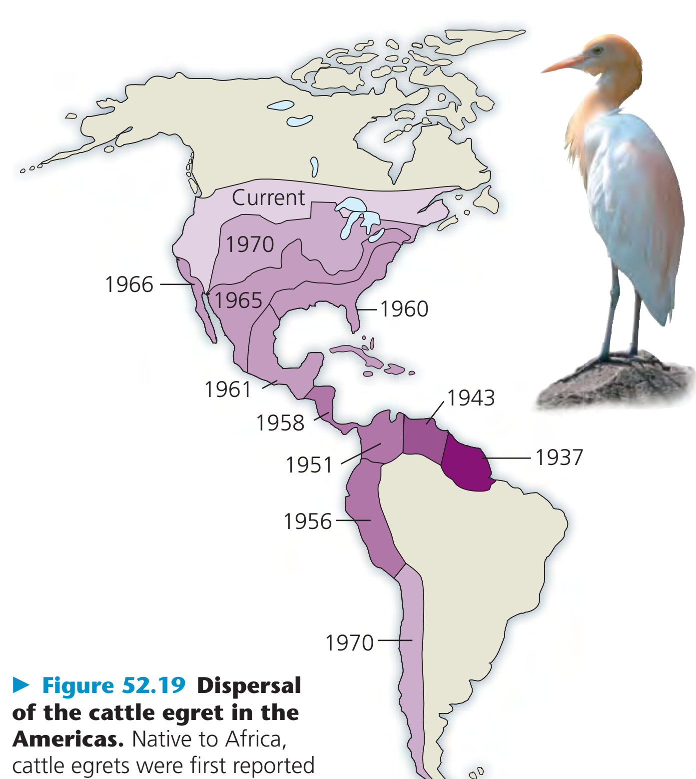
Dispersal and Distribution

One factor that contributes greatly to the global distribution of organisms is **dispersal**, the movement of individuals or gametes away from their area of origin or from centers of high population density. A biogeographer who studies the distributions of species in the context of evolutionary theory might consider dispersal in hypothesizing why there are no kangaroos in North America: A barrier may have kept them from reaching the continent. While land-bound kangaroos have not reached North America under their own power, other organisms that disperse more readily, such as some birds, have. The dispersal of organisms is critical to understanding the role of geographic isolation in evolution (see Chapter 24) as well as the broad patterns of species distribution we see today, including that of the Pacific diatom discussed earlier in this chapter.

Natural Range Expansions and Adaptive Radiation

EVOLUTION The importance of dispersal is most evident when organisms reach an area where they did not exist previously. For instance, 200 years ago, the cattle egret (*Bubulcus ibis*) was found only in Africa and southwestern Europe. But in the late 1800s, some of these birds managed to cross the Atlantic Ocean and colonize northeastern South America. From there, cattle egrets gradually spread southward and also northward through Central America and into North America, reaching Florida by 1960 **(Figure 52.19)**. Today they have breeding populations as far west as the Pacific coast of the United States and as far north as southern Canada.

In rare cases, such long-distance dispersal can lead to adaptive radiation, the rapid evolution of an ancestral species into new species that fill many ecological niches (see Chapter 25). The incredible diversity of Hawaiian silverswords is an example of adaptive radiation that was possible only with the long-distance dispersal of an ancestral tarweed from North America (see Figure 25.20).



▶ **Figure 52.19 Dispersal of the cattle egret in the Americas.** Native to Africa, cattle egrets were first reported in South America in 1877.

Natural range expansions clearly show the influence of dispersal on distribution. However, opportunities to observe such dispersal directly are rare, so ecologists often turn to experimental methods to better understand the role of dispersal in limiting the distribution of species.

Species Transplants

To determine if dispersal is a key factor limiting the distribution of a species, ecologists may observe the results of intentional or accidental transplants of the species to areas where it was previously absent. For a transplant to be considered successful, some of the organisms must not only survive in the new area but also reproduce there sustainably. If a transplant is successful, then we can conclude that the *potential* range of the species is larger than its *actual* range; in other words, the species *could* live in certain areas where it currently does not.

Species introduced to new geographic locations often disrupt the communities and ecosystems to which they have been introduced and spread far beyond the area of introduction (see Chapter 56). Consequently, ecologists rarely move species to new geographic regions. Instead, they document the outcome when a species has been transplanted for other purposes, such as to introduce game animals or predators of pest species, or when a species has been accidentally transplanted.

Behavior and Habitat Selection

As transplant experiments show, some organisms do not occupy all of their potential range, even though they may be physically able to disperse into the unoccupied areas. To follow our line of questioning from Figure 52.18, does behavior play a role in limiting distribution in such cases? When individuals seem to avoid certain habitats, even when the habitats are suitable, the organism's distribution may be limited by habitat selection behavior.

Although habitat selection is one of the least understood of all ecological processes, some instances in insects have been closely studied. Female insects often deposit eggs only in response to a very narrow set of stimuli, which may restrict distribution of the insects to certain host plants. Larvae of the European corn borer, for example, can feed on a wide variety of plants but are found almost exclusively on corn (maize) because egg-laying females are attracted by odors produced by the plant. Habitat selection behavior clearly restricts this insect to geographic locations where corn is found.

Biotic Factors

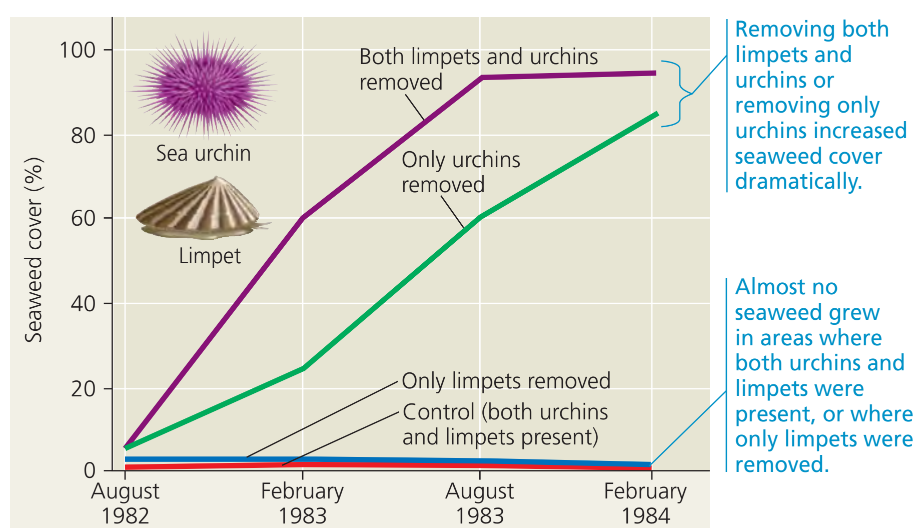
If behavior does not limit the distribution of a species, our next question is whether biotic factors—other species—are responsible. Often, negative interactions with predators (organisms that kill their prey) or herbivores (organisms that eat plants or algae) restrict the ability of a species to survive and reproduce. **Figure 52.20** describes a specific case of an herbivore, a sea urchin, limiting the distribution of a food species.

▼ Figure 52.20 **INQUIRY**

Does feeding by sea urchins limit seaweed distribution?

EXPERIMENT W. J. Fletcher, of the University of Sydney, Australia, reasoned that if sea urchins are a limiting biotic factor in a particular ecosystem, then more seaweeds should invade an area from which sea urchins have been removed. To isolate the effect of sea urchins from that of a seaweed-eating mollusc, the limpet, he removed only urchins, only limpets, or both from study areas adjacent to a control site.

RESULTS Fletcher observed a large difference in seaweed growth between areas with and without sea urchins.



CONCLUSION Removing both limpets and urchins resulted in the greatest increase in seaweed cover, indicating that both species have some influence on seaweed distribution. But since removing only urchins greatly increased seaweed growth while removing only limpets had little effect, Fletcher concluded that sea urchins have a much greater effect than limpets in limiting seaweed distribution.

SOURCE W. J. Fletcher, Interactions among subtidal Australian sea urchins, gastropods, and algae: effects of experimental removals, *Ecological Monographs* 57:89–109 (1989).

WHAT IF? Seaweed cover increased the most when both urchins *and* limpets were removed. How might you explain this result?

In certain marine ecosystems, there is often an inverse relationship between the abundance of sea urchins and seaweeds (multicellular algae, such as kelp). Where urchins that graze on seaweeds and other algae are common, large stands of seaweeds do not become established. As described in Figure 52.20, Australian researchers have tested the hypothesis that sea urchins are a biotic factor limiting seaweed distribution. When sea urchins were removed from experimental plots, seaweed cover increased dramatically, showing that urchins limited the distribution of seaweeds.

In addition to predation and herbivory, the presence or absence of pollinators, food resources, parasites, pathogens, and competing organisms can act as a biotic limitation on species distribution. Some of the most striking cases of limitation occur when humans accidentally or intentionally introduce exotic predators or pathogens into new areas and wipe out native species. You will encounter examples of these impacts in Chapter 56, where we discuss conservation biology.

Abiotic Factors

The last question in the flowchart in Figure 52.18 considers whether abiotic factors, such as temperature, water, oxygen, salinity, sunlight, or soil, might be limiting a species' distribution. If the physical conditions at a site do not allow a species to survive and reproduce, then the species will not be found there. Throughout this discussion, keep in mind that most abiotic factors vary substantially in space and time. Daily and annual fluctuations of abiotic factors may either blur or accentuate regional distinctions. Furthermore, organisms can avoid some stressful conditions temporarily through behaviors such as dormancy or hibernation.

Temperature

Environmental temperature is an important factor in the distribution of organisms because of its effect on biological processes. Cells may rupture if the water they contain freezes (at temperatures below 0°C), and the proteins of most organisms denature at temperatures above 45°C. Most organisms function best within a specific range of environmental temperature. Temperatures outside that range may force some animals to expend energy regulating their internal temperature, as mammals and birds do (see Chapter 40). Extraordinary adaptations enable certain organisms, such as thermophilic prokaryotes (see Chapter 27), to live outside the temperature range habitable by other life.

Water and Oxygen

The dramatic variation in water availability among habitats is another important factor in species distribution. Species living at the seashore or in tidal wetlands can desiccate (dry out) as the tide recedes. Terrestrial organisms face a nearly constant threat of desiccation, and the distribution of terrestrial species reflects their ability to obtain and conserve water. Many amphibians, such as the harlequin toad in Figure 52.1, are particularly vulnerable to drying because they use their moist, delicate skin for gas exchange. Desert organisms exhibit a variety of adaptations for acquiring and conserving water in dry environments, as described in Chapter 44.

Water affects oxygen availability in aquatic environments and in flooded soils. Because oxygen diffuses slowly in water, its concentration can be low in certain aquatic systems and soils, limiting cellular respiration and other physiological processes. Oxygen concentrations can be particularly low in both deep ocean and deep lake waters and sediments where organic matter is abundant. Flooded wetland soils may also have low oxygen content. Mangroves and other trees have specialized roots that project above the water and help the root system obtain oxygen (see Figure 35.4). Unlike many flooded wetlands, the surface waters of streams and rivers tend to be well oxygenated because of rapid exchange of gases with the atmosphere.

Salinity

As you learned in Chapter 7, the salt concentration of water in the environment affects the water balance of organisms through osmosis. Most aquatic organisms are restricted to either freshwater or saltwater habitats by their limited ability to osmoregulate (see Chapter 44). Although most terrestrial organisms can excrete excess salts from specialized glands or in feces or urine, salt flats and other high-salinity habitats typically have few species of plants or animals.

Salmon that migrate between freshwater streams and the ocean use both behavioral and physiological mechanisms to osmoregulate. They adjust the amount of water they drink to help balance their salt content, and their gills switch from taking up salt in fresh water to excreting salt in the ocean.

Sunlight

Sunlight absorbed by photosynthetic organisms provides the energy that drives most ecosystems, and too little sunlight can limit the distribution of photosynthetic species. In forests, shading by leaves in the treetops makes competition for light especially intense, particularly for seedlings growing on the forest floor. In aquatic environments, every meter of water depth selectively absorbs about 45% of the red light and about 2% of the blue light passing through it. As a result, most photosynthesis in aquatic environments occurs relatively near the surface.

▲ **Figure 52.21 Alpine tree line in Banff National Park, Canada.** Organisms living at high elevations are exposed not only to high levels of ultraviolet radiation but also to freezing temperatures, moisture deficits, and strong winds. Above the tree line, the combination of such factors restricts the growth and survival of trees.

Too much light can also limit the survival of organisms. In some ecosystems, such as deserts, high light levels can increase temperature stress if animals and plants are unable to avoid the light or to cool themselves through evaporation (see Chapter 40). At high elevations, the sun's rays are more likely to damage DNA and proteins because the atmosphere is thinner, absorbing less ultraviolet (UV) radiation. Damage from UV radiation, combined with other abiotic stresses, prevents trees from surviving above a certain elevation, resulting in the appearance of a tree line on mountain slopes **(Figure 52.21)**.

Rocks and Soil

In terrestrial environments, the pH, mineral composition, and physical structure of rocks and soil limit the distribution of plants and thus of the animals that feed on them, contributing to the patchiness of terrestrial ecosystems. The pH of soil can limit the distribution of organisms directly, through extreme acidic or basic conditions, or indirectly, by affecting the solubility of nutrients and toxins.

In a river, the composition of the rocks and soil that make up the substrate (riverbed) can affect water chemistry, which in turn influences the resident organisms. In freshwater and marine environments, the structure of the substrate determines the organisms that can attach to it or burrow into it.

Throughout this chapter, you have seen how the distributions of biomes and organisms depend on abiotic and biotic factors. In the next chapter, we continue to work our way through the hierarchy outlined in Figure 52.2, focusing on how abiotic and biotic factors influence the ecology of populations.

CONCEPT CHECK 52.4

1. Give examples of human actions that could expand a species' distribution by changing its (a) dispersal or (b) biotic interactions.
2. **WHAT IF?** You suspect that deer are restricting the distribution of a tree species by preferentially eating the seedlings of the tree. How might you test this hypothesis?
3. **MAKE CONNECTIONS** As you saw in Figure 25.20 (p. 525), Hawaiian silverswords underwent a remarkable adaptive radiation after their ancestor reached Hawaii, while the islands were still young. Would you expect the cattle egret to undergo a similar adaptive radiation in the Americas (see Figure 52.19)? Explain.

For suggested answers, see Appendix A.

52 CHAPTER REVIEW

SUMMARY OF KEY CONCEPTS

CONCEPT 52.1

Earth's climate varies by latitude and season and is changing rapidly (pp. 1144–1150)

- Global **climate** patterns are largely determined by the input of solar energy and Earth's revolution around the sun.
- The changing angle of the sun over the year, bodies of water, and mountains exert seasonal, regional, and local effects on **macroclimate**.
- Fine-scale differences in **abiotic** (nonliving) factors, such as sunlight and temperature, determine **microclimate**.
- Increasing greenhouse gas concentrations in the air are warming Earth and altering the distributions of many species. Some species will not be able to shift their ranges quickly enough to reach suitable habitat in the future.

? *Suppose global air circulation suddenly reversed, with most air ascending at 30° north and south latitude and descending at the equator. At what latitude would you most likely find deserts in this scenario?*

CONCEPT 52.2

The structure and distribution of terrestrial biomes are controlled by climate and disturbance (pp. 1150–1156)

- **Climographs** show that temperature and precipitation are correlated with **biomes**. Because other factors also play roles in biome location, biomes overlap.
- Terrestrial biomes are often named for major physical or climatic factors and for their predominant vegetation. Vertical layering is an important feature of terrestrial biomes.
- **Disturbance**, both natural and human-induced, influences the type of vegetation found in biomes. Humans have altered much of Earth's surface, replacing the natural terrestrial communities described and depicted in Figure 52.12 with urban and agricultural ones.

? *Some arctic tundra ecosystems receive as little rainfall as deserts but have much more dense vegetation. Based on Figure 52.10, what climatic factor might explain this difference? Explain.*

CONCEPT 52.3

Aquatic biomes are diverse and dynamic systems that cover most of Earth (pp. 1157–1163)

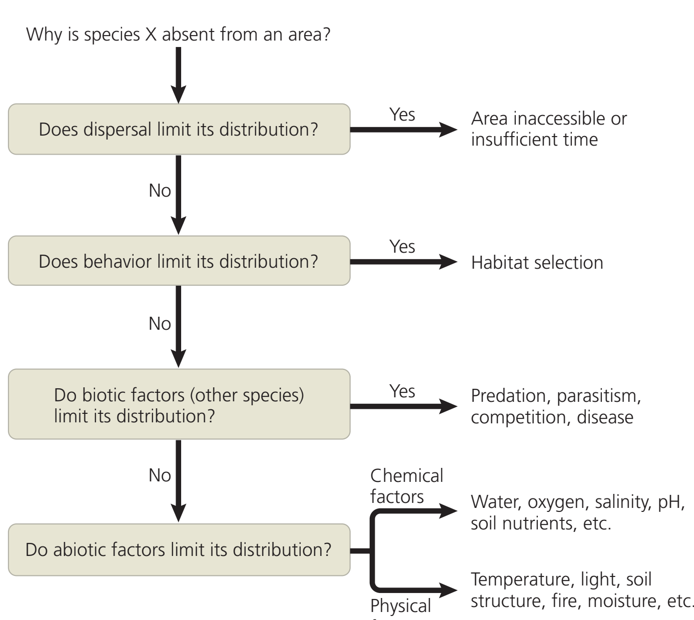
- Aquatic biomes are characterized primarily by their physical environment rather than by climate and are often layered with regard to light penetration, temperature, and community structure. Marine biomes have a higher salt concentration than freshwater biomes.
- In the ocean and in most lakes, an abrupt temperature change called a **thermocline** separates a more uniformly warm upper layer from more uniformly cold deeper waters.

? *In which aquatic biomes might you find an aphotic zone?*

CONCEPT 52.4

Interactions between organisms and the environment limit the distribution of species (pp. 1163–1167)

- Ecologists want to know not only *where* species occur but also *why* those species occur where they do.



- The distribution of species may be limited by **dispersal**, the movement of individuals away from their area of origin; behavior; **biotic** (living) factors; and abiotic factors, such as temperature extremes, salinity, and water availability.

? *If you were an ecologist studying the chemical and physical limits to the distributions of species, how might you rearrange the flowchart preceding this question?*

TEST YOUR UNDERSTANDING

LEVEL 1: KNOWLEDGE/COMPREHENSION

1. Which of the following areas of study focuses on the exchange of energy, organisms, and materials between ecosystems?
   a. population ecology
   b. organismal ecology
   c. landscape ecology
   d. ecosystem ecology
   e. community ecology
2. Which lake zone would be absent in a very shallow lake?
   a. benthic zone
   b. aphotic zone
   c. pelagic zone
   d. littoral zone
   e. limnetic zone
3. Which of the following is true with respect to oligotrophic lakes and eutrophic lakes?
   a. Oligotrophic lakes are more subject to oxygen depletion.
   b. Rates of photosynthesis are lower in eutrophic lakes.
   c. Eutrophic lake water contains lower concentrations of nutrients.
   d. Eutrophic lakes are richer in nutrients.
   e. Sediments in oligotrophic lakes contain larger amounts of decomposable organic matter.
4. Which of the following biomes is correctly paired with the description of its climate?
   a. savanna—low temperature, precipitation uniform during the year
   b. tundra—long summers, mild winters
   c. temperate broadleaf forest—relatively short growing season, mild winters
   d. temperate grasslands—relatively warm winters, most rainfall in summer
   e. tropical forests—nearly constant day length and temperature

LEVEL 2: APPLICATION/ANALYSIS

5. Which of the following is characteristic of most terrestrial biomes?
   a. annual average rainfall in excess of 250 cm
   b. a distribution predicted almost entirely by rock and soil patterns
   c. clear boundaries between adjacent biomes
   d. vegetation demonstrating vertical layering
   e. cold winter months
6. The oceans affect the biosphere in all of the following ways *except*
   a. producing a substantial amount of the biosphere's oxygen.
   b. removing carbon dioxide from the atmosphere.
   c. moderating the climate of terrestrial biomes.
   d. regulating the pH of freshwater biomes and terrestrial groundwater.
   e. being the source of most of Earth's rainfall.

7. Which statement about dispersal is *false*?
   a. Dispersal is a common component of the life cycles of plants and animals.
   b. Colonization of devastated areas after floods or volcanic eruptions depends on dispersal.
   c. Dispersal occurs only on an evolutionary time scale.
   d. Seeds are important dispersal stages in the life cycles of most flowering plants.
   e. The ability to disperse can expand the geographic distribution of a species.

8. When climbing a mountain, we can observe transitions in biological communities that are analogous to the changes
   a. in biomes at different latitudes.
   b. at different depths in the ocean.
   c. in a community through different seasons.
   d. in an ecosystem as it evolves over time.
   e. across the United States from east to west.

9. Suppose that the number of bird species is determined mainly by the number of vertical strata found in the environment. If so, in which of the following biomes would you find the greatest number of bird species?
   a. tropical rain forest
   b. savanna
   c. desert
   d. temperate broadleaf forest
   e. temperate grassland

LEVEL 3: SYNTHESIS/EVALUATION

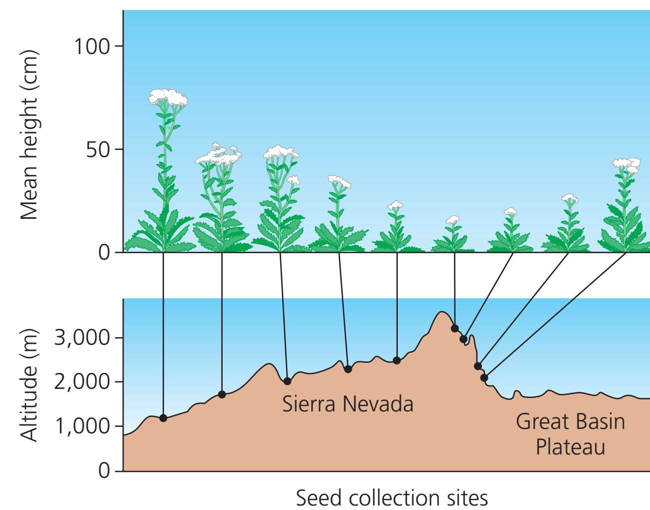
10. **WHAT IF?** If the direction of Earth's rotation reversed, the most predictable effect would be
    a. no more night and day.
    b. a big change in the length of the year.
    c. winds blowing from west to east along the equator.
    d. a loss of seasonal variation at high latitudes.
    e. the elimination of ocean currents.

11. **DRAW IT** After reading about the experiment of W. J. Fletcher described in Figure 52.20, you decide to study feeding relationships among sea otters, sea urchins, and kelp on your own. You know that sea otters prey on sea urchins and that urchins eat kelp. At four coastal sites, you measure kelp abundance. Then you spend one day at each site and mark whether otters are present or absent every 5 minutes during daylight hours. Make a graph that shows how otter density depends on kelp abundance, using the data shown below. Then formulate a hypothesis to explain the pattern you observed.

Site	Kelp Abundance (% cover)	Otter Density (# sightings per day)
1	75	98
2	15	18
3	60	85
4	25	36

12. **EVOLUTION CONNECTION**
    Discuss how the concept of time applies to ecological situations and evolutionary changes. Do ecological time and evolutionary time ever overlap? If so, what are some examples?

13. **SCIENTIFIC INQUIRY**
    Jens Clausen and colleagues, at the Carnegie Institution of Washington, studied how the size of yarrow plants (*Achillea lanulosa*) growing on the slopes of the Sierra Nevada varied with elevation. They found that plants from low elevations were generally taller than plants from high elevations, as shown below:



Source: J. Clausen et al., Experimental studies on the nature of species. III. Environmental responses of climatic races of *Achillea*, Carnegie Institution of Washington Publication No. 581 (1948).

Clausen and colleagues proposed two hypotheses to explain this variation within a species: (1) There are genetic differences between populations of plants found at different elevations. (2) The species has developmental flexibility and can assume tall or short growth forms, depending on local abiotic factors. If you had seeds from yarrow plants found at low and high elevations, what experiments would you perform to test these hypotheses?

14. **WRITE ABOUT A THEME**
    Feedback Regulation Global warming is occurring rapidly in Arctic marine and terrestrial ecosystems, including tundra and northern coniferous forests. In such locations, reflective white snow and ice cover are melting more quickly and extensively, uncovering darker-colored ocean water, plants, and rocks. In a short essay (100–150 words), explain how this process might represent a positive-feedback loop.

For selected answers, see Appendix A.

MasteringBIOLOGY® www.masteringbiology.com

1. MasteringBiology® Assignments

Tutorial Aquatic Biomes
Activities Tropical Atmospheric Circulation • Terrestrial Biomes • Adaptations to Biotic and Abiotic Factors • Discovery Channel Video: Trees
Questions Student Misconceptions • Reading Quiz • Multiple Choice • End-of-Chapter

2. eText

Read your book online, search, take notes, highlight text, and more.

3. The Study Area

Practice Tests • Cumulative Test • BioFlix 3-D Animations • MP3 Tutor Sessions • Videos • Activities • Investigations • Lab Media • Audio Glossary • Word Study Tools • Art