52 An Introduction to Ecology and the Biosphere

▲ **Figure 52.1 Why do gray whales migrate?**

KEY CONCEPTS

- **52.1 Ecology integrates all areas of biological research and informs environmental decision making**
- **52.2 Interactions between organisms and the environment limit the distribution of species**
- **52.3 Aquatic biomes are diverse and dynamic systems that cover most of Earth**
- **52.4 The structure and distribution of terrestrial biomes are controlled by climate and disturbance**

OVERVIEW

The Scope of Ecology

High in the sky, a series of satellites circle Earth. These satellites aren't relaying the chatter of cell phones. Instead, they are transmitting data on the annual migration of gray whales **(Figure 52.1)**. Leaving their calving grounds near Baja California, adult and newborn gray whales (*Eschrichtius robustus*) swim side by side on a remarkable 8,000-km journey. They are headed to the Arctic Ocean to feed on the crustaceans, tube worms, and other creatures that thrive there in summer. The satellites also help biologists track a second journey, the recovery of the gray whales from the brink of extinction. A century ago, whaling had reduced the population to only a few hundred individuals. Today, after 70 years of protection from whaling, more than 20,000 travel to the Arctic each year.

What environmental factors determine the geographic distribution of gray whales? How do variations in their food supply affect the size of the gray whale population? Questions such as these are the subject of **ecology** (from the Greek *oikos*, home, and *logos*, to study), the scientific study of the interactions between organisms and the environment. These interactions occur at a hierarchy of scales that ecologists study, from organismal to global **(Figure 52.2)**.

In addition to providing a conceptual framework for understanding the field of ecology, Figure 52.2 provides the organizational framework for our final unit. This chapter begins the unit by describing the breadth of ecology and some of the factors, both living and nonliving, that influence the distribution and abundance of organisms. The next three chapters examine population, community, and ecosystem ecology in detail. In the final chapter, we'll explore both landscape ecology and global ecology as we consider how ecologists apply biological knowledge to predict the global consequences of human activities, to conserve Earth's biodiversity, and to restore our planet's ecosystems.

CONCEPT **52.1**

Ecology integrates all areas of biological research and informs environmental decision making

Ecology's roots are in discovery science (see Chapter 1). Naturalists, including Aristotle and Darwin, have long observed organisms in nature and systematically recorded their observations. Because extraordinary insight can be gained through this descriptive approach, called *natural history*, it remains a fundamental part of the science of ecology. Present-day ecologists still observe the natural world, albeit with genes-to-globe tools that would astound Aristotle and Darwin.

Modern ecology has become a rigorous experimental science as well. Ecologists generate hypotheses, manipulate the environment, and observe the outcome. Scientists interested in the effects of climate change on tree survival, for instance, might create drought and wet conditions in experimental plots instead

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 in the biological hierarchy.

1 Organismal Ecology

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

◀ *How do hammerhead sharks select a mate?*

2 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 deer mice?*

3 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?*

4 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?*

5 Landscape Ecology

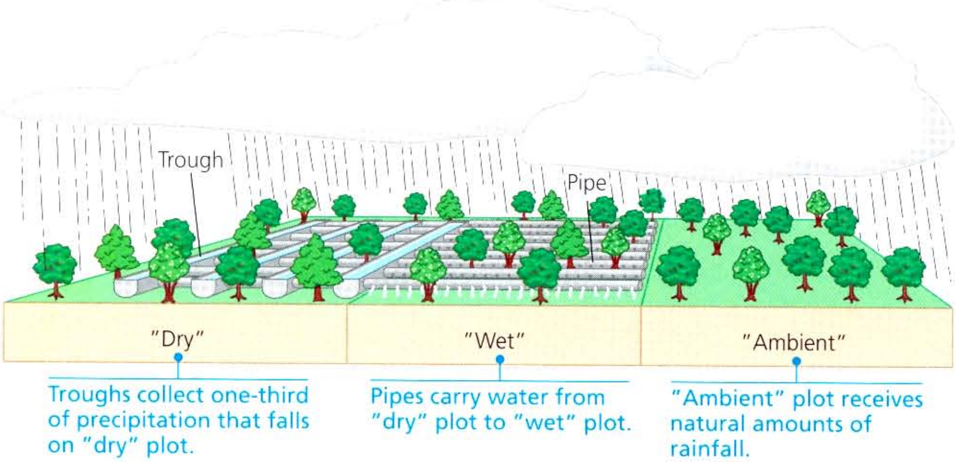
A **landscape** (or seascape) is a mosaic of connected ecosystems. Research in **landscape ecology** focuses on the factors controlling exchanges of energy, materials, and organisms across multiple ecosystems.

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

6 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?*



▲ **Figure 52.3 Studying how a forest responds to altered precipitation.** At the Walker Branch Watershed in Tennessee, researchers used a system of troughs and pipes to create artificial "dry" and "wet" conditions within parts of a forest.

of waiting decades for the dry or wet years that could be representative of future rainfall. Paul Hanson and colleagues, at Oak Ridge National Laboratory in Tennessee, used just such an experimental approach in a Herculean study that lasted more than ten years. In one large plot of native forest, they collected one-third of the incoming precipitation and moved it to a second plot, while leaving a third plot unchanged as a control **(Figure 52.3)**. By comparing the growth and survival of trees in each plot, the researchers found that flowering dogwoods (*Cornus florida*) were more likely to die in drought conditions than were members of any other woody species examined.

Throughout this unit, you will encounter many more examples of ecological field experiments, whose complex challenges have made ecologists innovators in the areas of experimental design and statistical inference. As these examples also demonstrate, the interpretation of ecological experiments often depends on a broad knowledge of biology.

Linking Ecology and Evolutionary Biology

As we discussed in Chapter 23, organisms adapt to their environment over many generations through the process of natural selection; this adaptation occurs over many generations—the time frame of *evolutionary time*. The differential survival and reproduction of individuals that leads to evolution occurs in *ecological time*, the minute-to-minute time frame of interactions between organisms and the environment. One example of how events in ecological time have led to evolution was the selection for beak size in Galápagos finches (see Figure 23.1). Finches with bigger beaks were better able to eat the large, hard seeds available during the drought. Smaller-beaked birds, which required smaller, softer seeds that were in short supply, were less likely to survive.

We can see the link between ecology and evolution all around us. Suppose a farmer applies a new fungicide to protect a wheat crop from a fungus. The fungicide works well at first, reducing the population size of the fungus—an ecological effect—and allowing the farmer to obtain higher yields from the crop. After a few years, however, the farmer has to apply higher and higher doses of the fungicide to obtain the same protection. The fungicide has altered the gene pool of the fungus—an evolutionary effect—by selecting for individuals that are resistant to the chemical. Eventually, the fungicide works so poorly that the farmer must find a different, more potent chemical to control the fungus.

Ecology and Environmental Issues

Ecology and evolutionary biology help us understand the emergence of pesticide-resistant organisms and many other environmental problems. Ecology also provides the scientific understanding needed to help us conserve and sustain life on Earth. Because of ecology's usefulness in conservation and environmental efforts, many people associate ecology with *environmentalism* (advocating the protection of nature).

Ecologists make an important distinction between science and advocacy. Many ecologists feel a responsibility to educate legislators and the public about environmental issues. How society uses ecological knowledge, however, depends on much more than science alone. If we know that phosphate promotes the growth of algae in lakes, for instance, policymakers may weigh the environmental benefits of limiting the use of phosphate-rich fertilizers against the costs of doing so. This distinction between knowledge and advocacy is clear in the guiding principles of the Ecological Society of America, a scientific organization that strives to "ensure the appropriate use of ecological science in environmental decision making."

An important milestone in applying ecological data to environmental problems was the publication of Rachel Carson's *Silent Spring* in 1962 **(Figure 52.4)**. In her book, which

◀ **Figure 52.4 Rachel Carson.**

was seminal to the modern environmental movement, Carson (1907–1964) had a broad message: "The 'control of nature' is a phrase conceived in arrogance, born of the Neanderthal age of biology and philosophy, when it was supposed that nature exists for the convenience of man." Recognizing the network of connections among species, Carson warned that the widespread use of pesticides such as DDT was causing population declines in many more organisms than the insects targeted for control. She applied ecological principles to recommend a less wasteful, safer use of pesticides. Through her writing and her testimony before the U.S. Congress, Carson helped promote a new environmental ethic to lawmakers and the public. Her efforts led to a ban on DDT use in the United States and more stringent controls on the use of other chemicals.

CONCEPT CHECK 52.1

1. Contrast the terms *ecology* and *environmentalism*. How does ecology relate to environmentalism?
2. How can an event that occurs on the ecological time scale affect events that occur on an evolutionary time scale?
3. **WHAT IF?** A wheat farmer tests four fungicides on small plots and finds that the wheat yield is slightly higher when all four fungicides are used together than when any one fungicide is used alone. From an evolutionary perspective, what would be the likely long-term consequence of applying all four fungicides together?

For suggested answers, see Appendix A.

CONCEPT 52.2

Interactions between organisms and the environment limit the distribution of species

Earlier we introduced the range of scales at which ecologists work and explained how ecology can be used to understand, and make decisions about, our environment. In this section, we will examine how ecologists determine what controls the distribution of species, such as the gray whale in Figure 52.1.

In Chapter 22, we explored *biogeography*, the study of the past and present distribution of species, in the context of evolutionary theory. Ecologists have long recognized global and regional patterns in the distribution of organisms. 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 two kinds of factors: **biotic**, or living, factors—all the organisms that are part of the individual's environment—and **abiotic**, or nonliving, factors—all the chemical and physical factors, such as temperature, light, water, and nutrients, that influence the distribution and abundance of organisms.

Figure 52.5 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, where

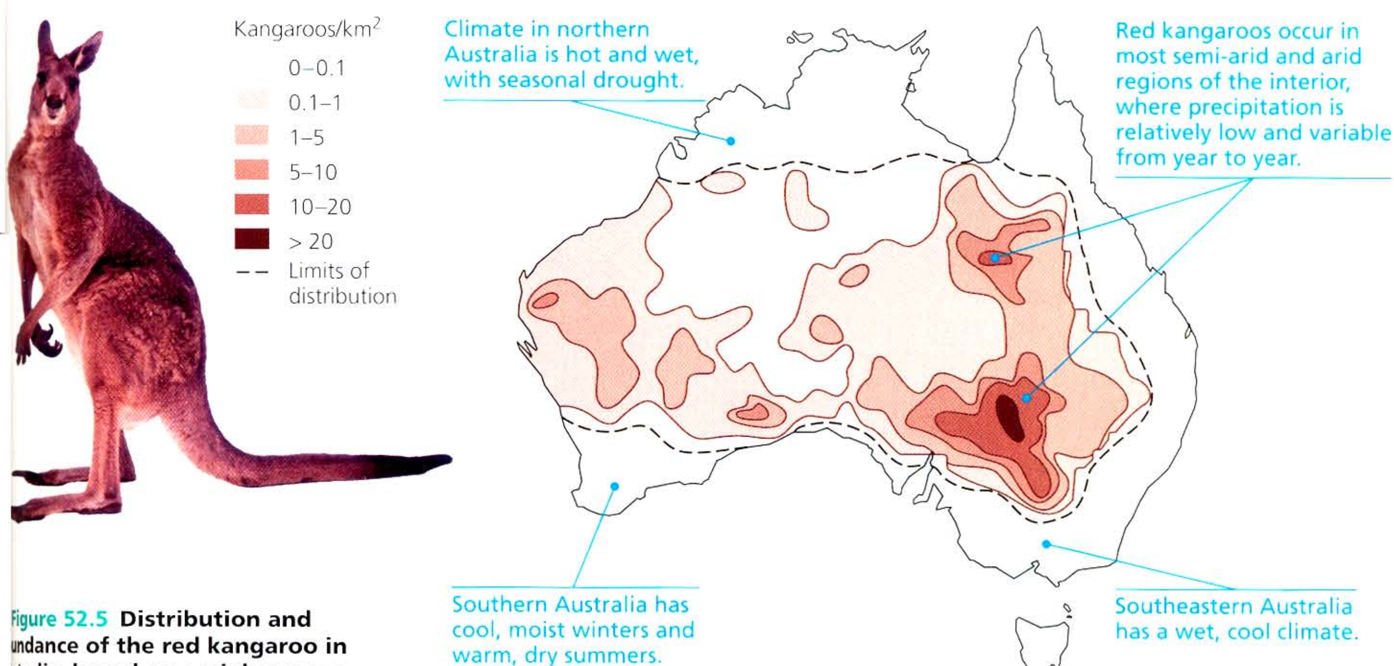
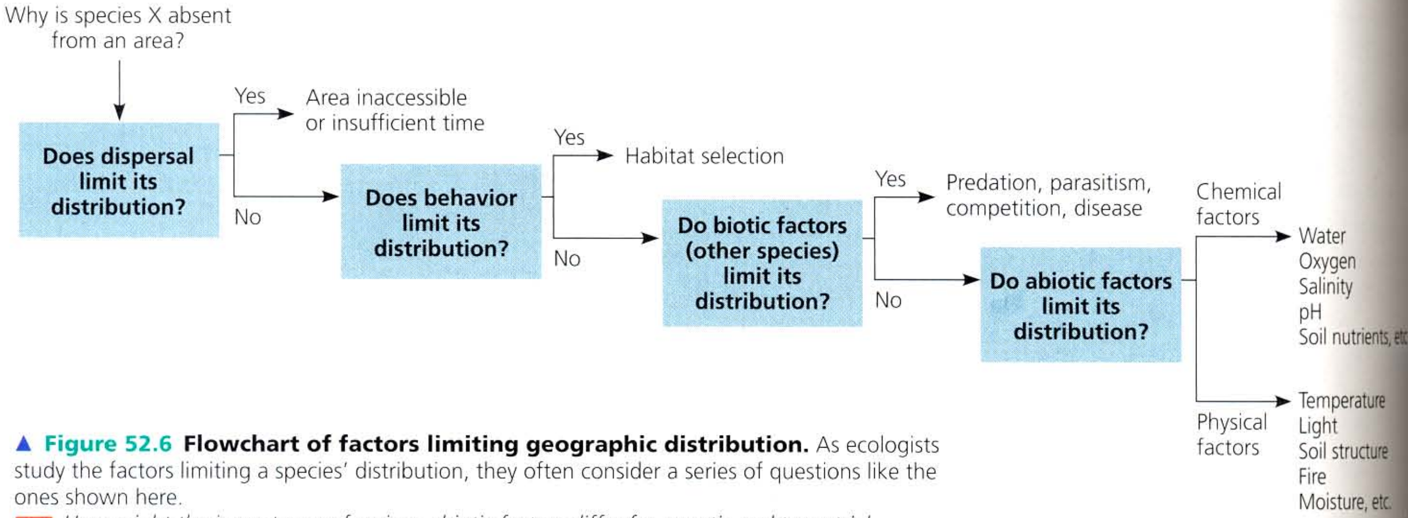


Figure 52.5 Distribution and undance of the red kangaroo in stralia, based on aerial surveys.



▲ **Figure 52.6 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?*

the climate ranges from moist to wet. At first glance, this distribution might suggest that an abiotic factor—the amount and variability of precipitation—directly determines where red kangaroos live. However, it is also possible that climate influences 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 52.6.**

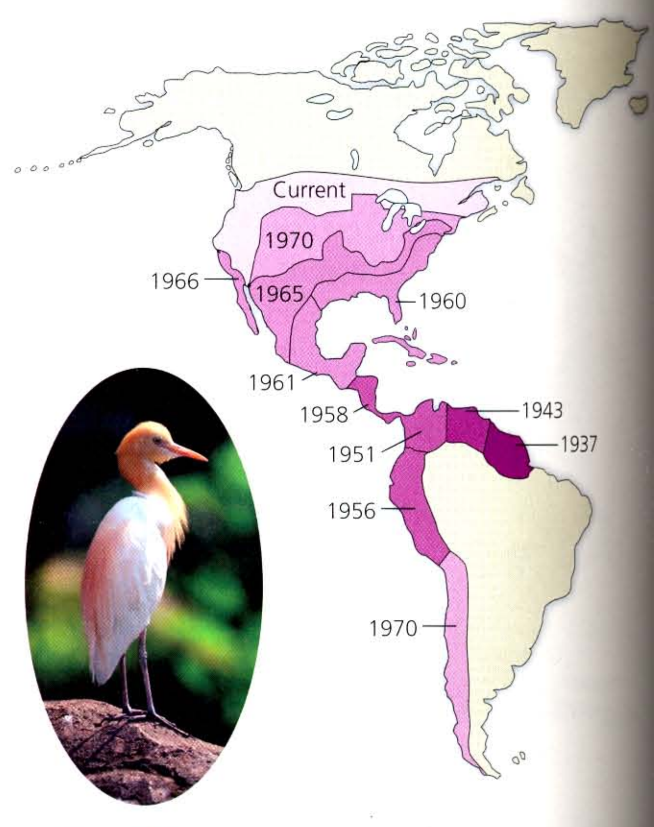
Dispersal and Distribution

The movement of individuals away from their area of origin or from centers of high population density, called **dispersal**, contributes to the global distribution of organisms. A biogeographer might consider dispersal in hypothesizing why there are no kangaroos in North America: Kangaroos could not get there because a barrier to their dispersal existed. 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 both geographic isolation in evolution (see Chapter 24) and the broad patterns of current geographic distributions of species.

Natural Range Expansions

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 was found only in Africa and southwestern Europe. But in the late 1800s, some of these strong-flying 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 52.7)**. Today they have breeding populations as far west as the Pacific coast of the United States and as far north as southern Canada.

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



▲ **Figure 52.7 Dispersal of the cattle egret in the Americas.** Native to Africa, cattle egrets were first reported in South America in 1877.

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. 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 intended introduction (see Chapter 56). Consequently, ecologists rarely conduct transplant experiments across 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 52.6, 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 the plant species on which the corn borer is found.

Biotic Factors

If behavior does not limit the distribution of a species, our next question is whether biotic factors—that is, other species—are responsible (see Figure 52.6). In many cases, a species cannot complete its full life cycle if transplanted to a new area. This inability to survive and reproduce may be due to negative interactions with other organisms in the form of predation, parasitism, or competition. Alternatively, survival and reproduction may be limited by the absence of other species on which the transplanted species depends, such as pollinators for many flowering plants. Predators (organisms that kill their prey) and herbivores (organisms that eat plants or algae) are common examples of biotic factors that limit the distribution of species. Simply put, organisms that eat can limit the distribution of organisms that get eaten.

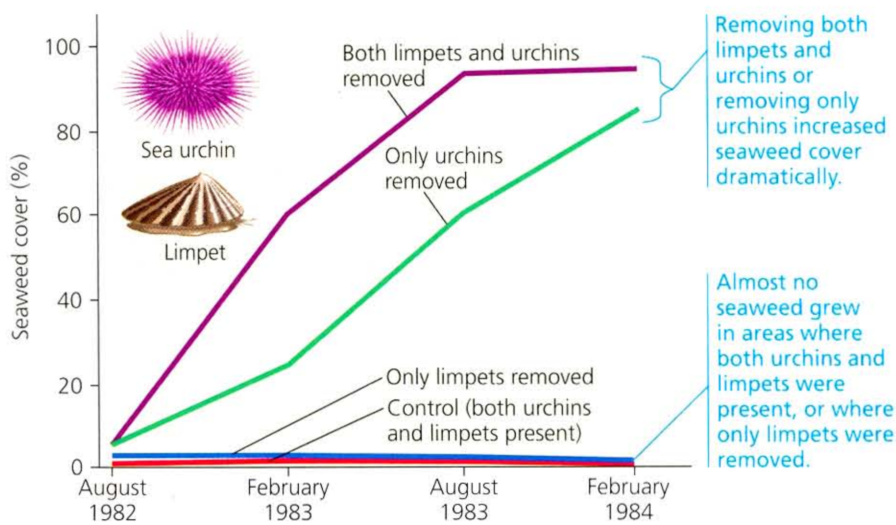
Let's examine one specific case of an herbivore limiting the distribution of a food species **(Figure 52.8)**. In certain marine ecosystems, there is often an inverse relationship between the abundance of sea urchins and seaweeds (large marine algae, such as kelp). Where sea urchins that graze on

▼ **Figure 52.8 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, then more seaweeds should invade an area from which sea urchins have been removed. To isolate the effect of sea urchins from that of another seaweed-eating animal, 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?

seaweeds and other algae are common, large stands of seaweeds do not become established. Thus, sea urchins appear to limit the local distribution of seaweeds. This kind of interaction can be tested by "removal and addition" experiments. In studies near Sydney, Australia, W. J. Fletcher tested the hypothesis that sea urchins are a biotic factor limiting seaweed distribution. Because there are often other herbivores in the habitats where seaweeds may grow, Fletcher performed a series of manipulative field experiments to isolate the influence of sea urchins on seaweeds in his study area (see Figure 52.8). By removing sea urchins from certain plots and observing the dramatic increase in seaweed cover, he showed that urchins limited the distribution of seaweeds.

In addition to predation and herbivory, the presence or absence of food resources, parasites, pathogens, and competing organisms can act as biotic limitations 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, which discusses conservation ecology.

Abiotic Factors

The last question in the flowchart in Figure 52.6 considers whether abiotic factors, such as temperature, water, 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 the environment is characterized by both *spatial heterogeneity* and *temporal heterogeneity*; that is, most abiotic factors vary in space and time. Although two regions of Earth may experience different conditions at any given 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. In addition, few organisms can maintain an active metabolism at very low or very high temperatures, though extraordinary adaptations enable some organisms, such as thermophilic prokaryotes (see Chapter 27), to live outside the temperature range habitable by other life. 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).

Water

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. Desert organisms, for example, exhibit a variety of adaptations for acquiring and conserving water in dry environments, as described in Chapter 44.

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 many terrestrial organisms can excrete excess salts from specialized glands or in feces, salt flats and other high-salinity habitats typically have few species of plants or animals.

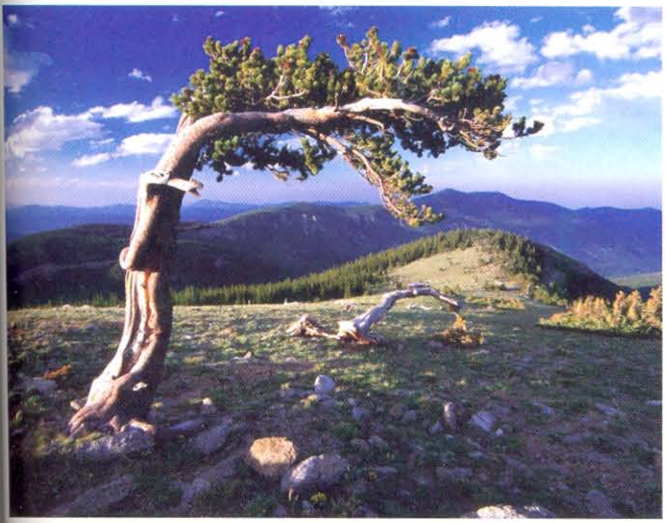
Sunlight

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.

Too much light can also limit the survival of organisms. The atmosphere is thinner at higher elevations, absorbing less ultraviolet radiation, so the sun's rays are more likely to damage DNA and proteins in alpine environments **(Figure 52.9)**. In other ecosystems, such as deserts, high light levels can increase temperature stress if animals are unable to avoid the light or to cool themselves through evaporation (see Chapter 40).

Rocks and Soil

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 and water can limit the distribution of organisms directly, through extreme acidic or basic conditions, or indirectly, through the solubility of nutrients and toxins. In streams and rivers, the composition of the substrate (bottom surface) can affect water chemistry, which in turn influences the resident organisms. In freshwater and marine environments, the



▲ **Figure 52.9 Alpine tree.** Organisms living at high elevations are exposed to high levels of ultraviolet radiation. They face other challenges as well, including freezing temperatures and strong winds, which increase water loss and inhibit the growth of limbs on the windward side of trees.

structure of the substrate determines the organisms that can attach to it or burrow into it.

Now that we have surveyed some of the abiotic factors that affect the distribution of organisms, let's focus on how those factors vary with climate, as we consider the major role that climate plays in determining species distribution.

Climate

Four abiotic factors—temperature, precipitation, sunlight, and wind—are the major components of **climate**, the long-term, prevailing weather conditions in a particular area. Climatic factors, particularly temperature and water availability, have a major influence on the distribution of terrestrial organisms. We can describe climate patterns on two scales: **macroclimate**, patterns on the global, regional, and local level; and **microclimate**, very fine patterns, such as those encountered by the community of organisms that live beneath a fallen log. First let's consider Earth's macroclimate.

Global Climate Patterns

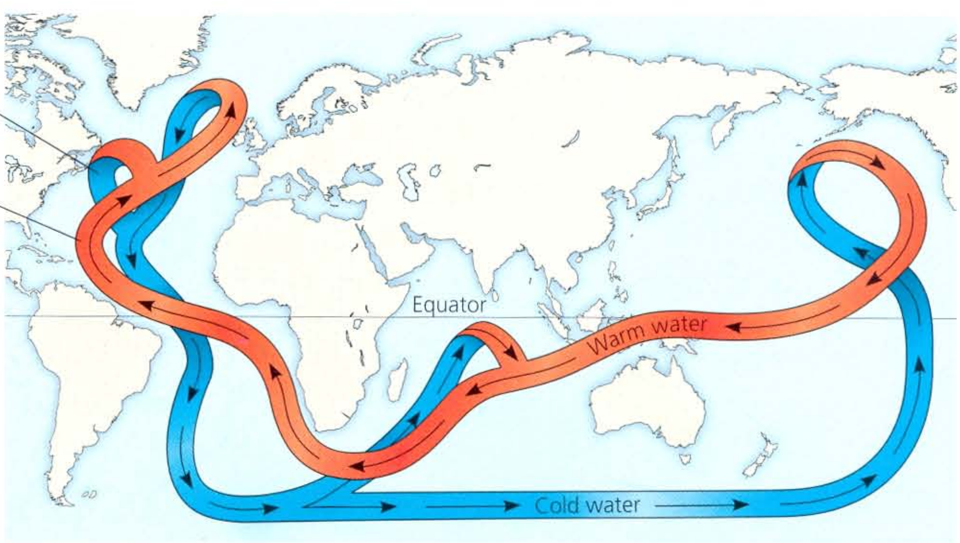
Earth's global climate patterns are determined largely by the input of solar energy and the planet's movement in space. The sun's warming effect on the atmosphere, land, and water establishes the temperature variations, cycles of air movement, and evaporation of water that are responsible for dramatic latitudinal variations in climate. **Figure 52.10**, on the next two pages, summarizes Earth's climate patterns and how they are formed.

Regional, Local, and Seasonal Effects on Climate

Proximity to bodies of water and topographic features such as mountain ranges create regional climatic variations, and smaller features of the landscape contribute to local climatic variation. Seasonal variation is another influence on climate.

Bodies of Water Ocean currents influence climate along the coasts of continents by heating or cooling overlying air masses, which may then pass across the land. Coastal regions are also generally moister than inland areas at the same latitude. The cool, misty climate produced by the cold California current that flows southward along the western United States supports a coniferous rain forest ecosystem in the Pacific Northwest and large redwood groves farther south. Similarly, the west coast of northern Europe has a mild climate because the Gulf Stream carries warm water from the equator to the North Atlantic, driven in part by the "great ocean conveyor belt" **(Figure 52.11)**. As a result, northwest Europe is warmer during winter than New England, 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 the land is warmer than the nearby body of water, air over the land heats up and



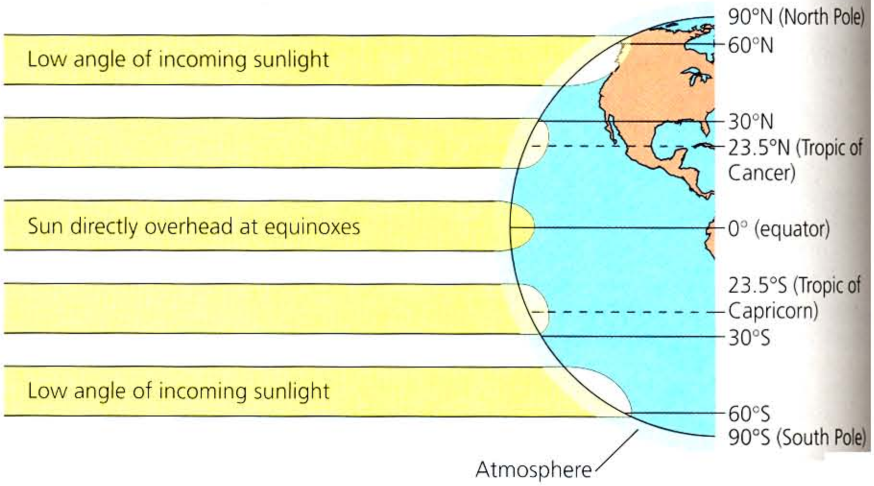
▲ **Figure 52.11 The great ocean conveyor belt.** Water is warmed at the equator and flows along the ocean surface to the North Atlantic, where it cools, becomes denser, and sinks thousands of meters. The deep, cold water may not return to the ocean surface for as long as 1,000 years.

▼ Figure 52.10

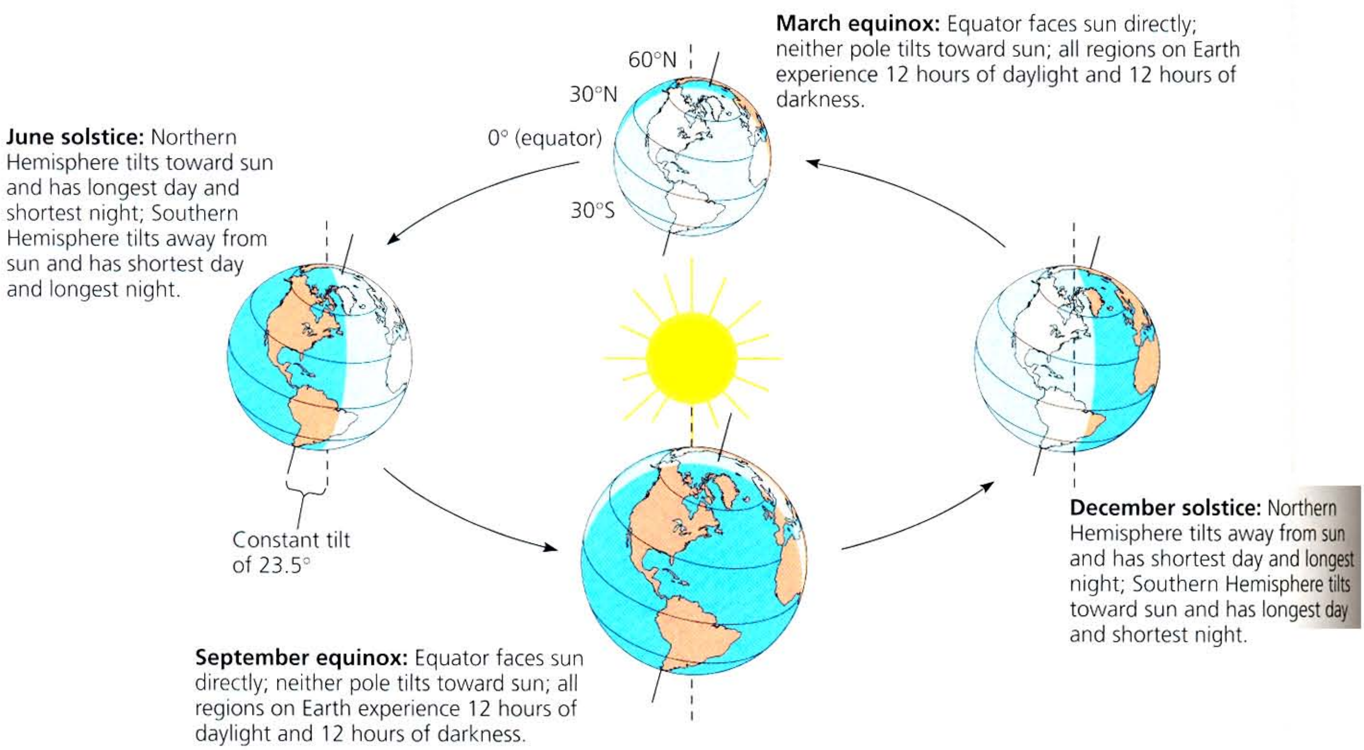
Exploring Global Climate Patterns

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.

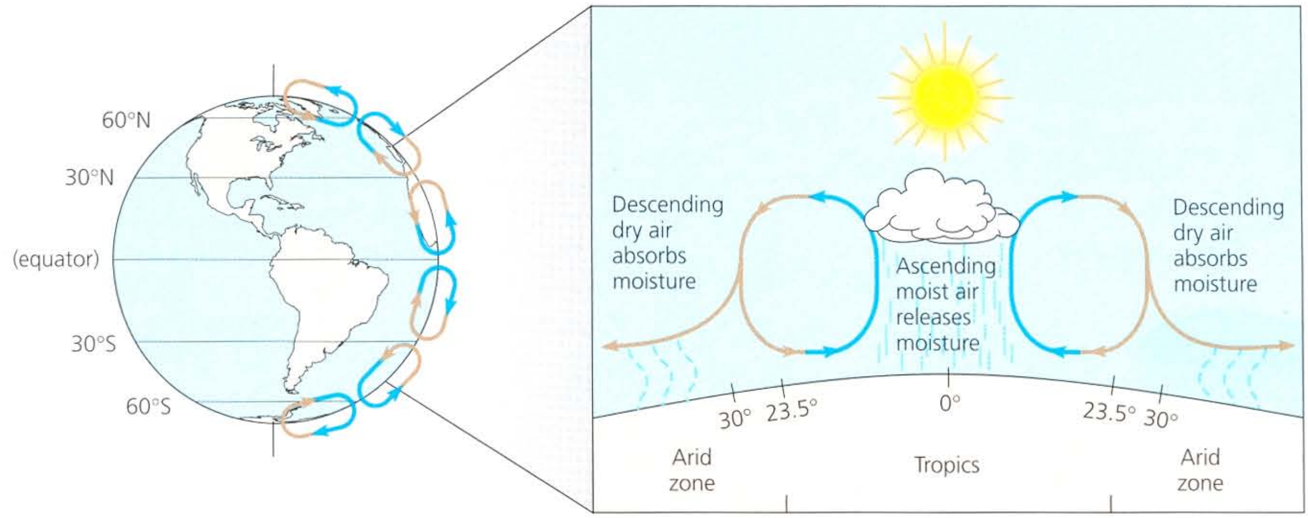


Seasonal Variation in Sunlight Intensity



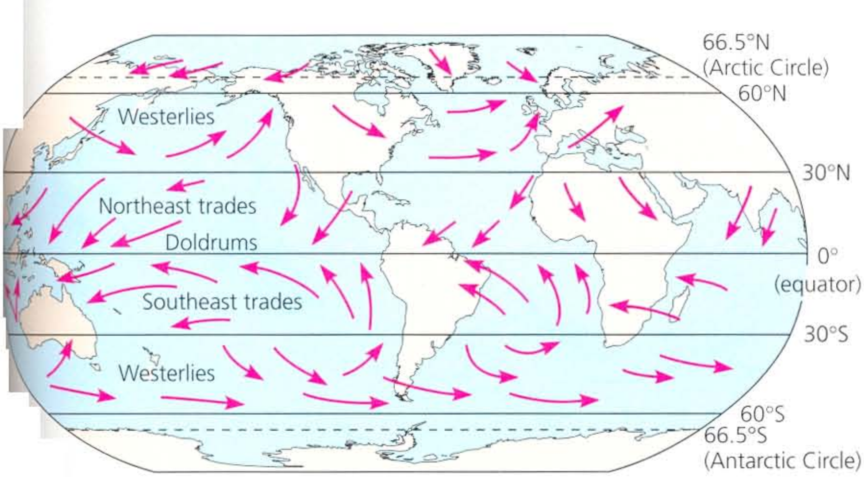
Earth's tilt causes seasonal variation in the intensity of solar radiation. Because the planet is tilted on its axis by 23.5° relative to its plane of orbit around the sun, the tropics experience the greatest annual input of solar radiation and the least seasonal variation. The seasonal variations of light and temperature increase toward the poles.

Global Air Circulation and Precipitation Patterns

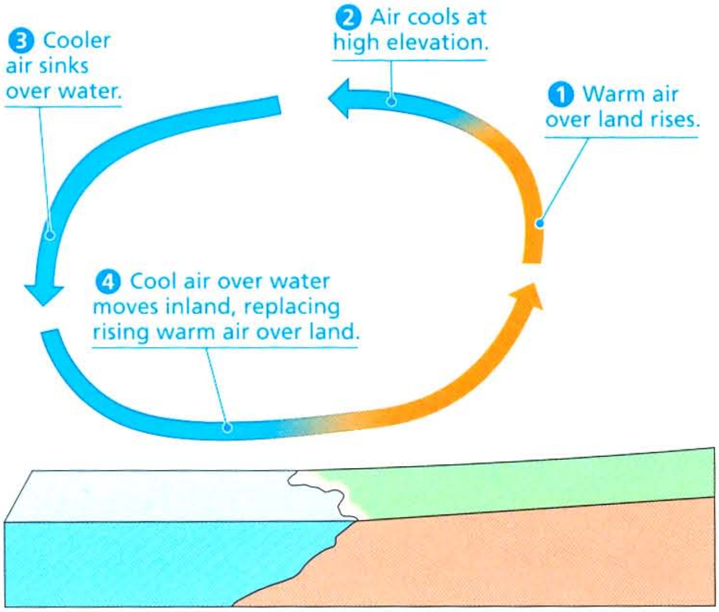


Intense solar radiation near the equator initiates a global pattern of air circulation and precipitation. High temperatures in the tropics evaporate water from Earth's surface and cause warm, wet air masses to rise (blue arrows) and flow toward the poles. The rising air masses release much of their water content, creating abundant precipitation in tropical regions. The high-altitude air masses, now dry, descend (brown arrows) toward Earth, absorbing moisture from the land and creating an arid climate conducive to the development of the deserts that are common at latitudes around 30° north and south. 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.

Global Wind Patterns



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 more easterly and westerly flows. 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.



▲ **Figure 52.12 Moderating effects of a large body of water on climate.** This figure illustrates what happens on a hot summer day.

rises, drawing a cool breeze from the water across the land **(Figure 52.12)**. At night, air over the now warmer water rises, drawing cooler air from the land back out over the water, replacing it with warmer air from offshore. The moderation of climate may be limited to the coast itself, however. In certain regions, such as southern California, 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*.

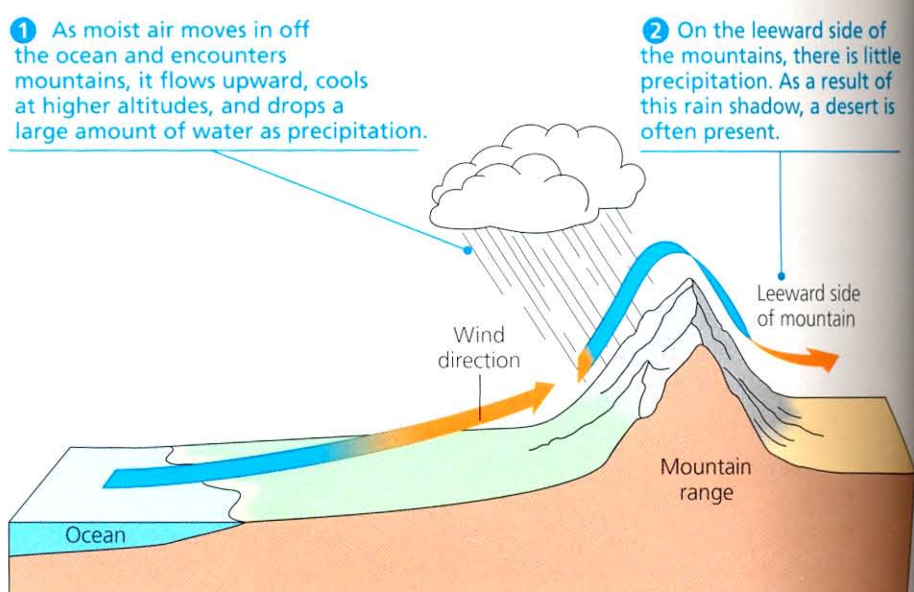
Mountains Mountains affect the amount of sunlight reaching an area and consequently the local temperature and rainfall. South-facing slopes in the Northern Hemisphere receive more sunlight than nearby north-facing slopes and are therefore warmer and drier. These abiotic differences influence species distribution; for example, in many mountains of western North America, spruce and other conifers occupy the cooler north-facing slopes, whereas shrubby, drought-resistant plants inhabit the south-facing slopes. In addition, every 1,000-m increase in elevation produces a temperature drop of approximately 6°C, equivalent to that produced by an 880-km increase in latitude. This is one reason the biological communities of mountains are similar to those at lower elevations but farther from the equator.

When warm, moist air approaches a mountain, the air rises and cools, releasing moisture on the windward side of the peak **(Figure 52.13)**. On the leeward side, cooler, dry air descends, absorbing moisture and producing a "rain shadow." Deserts commonly occur on the leeward side of mountain ranges, a phenomenon evident in 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.

Seasonality As described earlier, Earth's tilted axis of rotation and its annual passage around the sun cause strong seasonal cycles in middle to high latitudes (see Figure 52.10). 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 produce variations in 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.

Microclimate

Many features in the environment influence microclimates by casting shade, affecting evaporation from soil, or changing wind patterns. For example, forest trees frequently moderate the microclimate below them. Consequently, cleared areas generally experience greater temperature extremes than the



▲ **Figure 52.13 How mountains affect rainfall.**

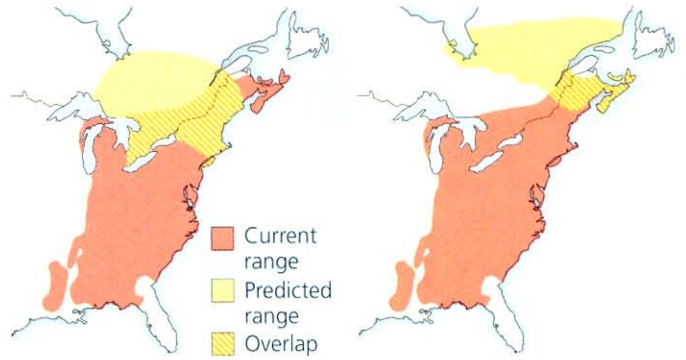
forest interior because of greater solar radiation and wind currents that are established by the rapid heating and cooling of open land. Within a forest, low-lying ground is usually wetter than high ground and tends to be occupied by different species of trees. A log or large stone can shelter organisms such as salamanders, worms, and insects, buffering them from the extremes of temperature and moisture. Every environment on Earth is similarly characterized by a mosaic of small-scale differences in the abiotic factors that influence the local distributions of organisms.

Long-Term Climate Change

If temperature and moisture are the most important factors limiting the geographic ranges of plants and animals, then the global climate change currently under way will profoundly affect the biosphere (see Chapter 55). One way to predict the possible effects of climate change 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 migrations is captured in fossil pollen deposited in lakes and ponds. (It may seem odd to think of trees "migrating," but recall from Chapter 38 that wind and animals can disperse seeds, sometimes over great distances.) If researchers can determine the climatic limits of current geographic distributions for organisms, they can make predictions about how distributions will change with climatic warming. A major question when applying this approach to plants is whether seed dispersal is rapid enough to sustain the migration of each species as climate changes. For example, fossils suggest that the eastern hemlock was delayed nearly 2,500 years in its movement north at the end of the last ice age. This delay in seed dispersal was partly attributable to the lack of "wings" on the seeds, causing the seeds to fall close to their parent tree.

Let's look at a specific case of how the fossil record of past tree migrations can inform predictions about the biological impact of the current global warming trend. **Figure 52.14** shows the current and predicted geographic ranges of the American beech (*Fagus grandifolia*) under two different climate-change models. These models predict that the northern limit of the beech's range will move 700–900 km northward in the next century, and its southern range limit will move northward an even greater distance. If these predictions are even approximately correct, the beech must move 7–9 km per year northward to keep pace with the warming climate. However, since the end of the last ice age, the beech has migrated into its present range at a rate of only 0.2 km per year. Without human assistance in moving into new ranges where they can survive as the climate warms, species such as the American beech may have much smaller ranges and may even become extinct.



(a) 4.5°C warming over next century

(b) 6.5°C warming over next century

▲ **Figure 52.14 Current range and predicted range for the American beech (*Fagus grandifolia*) under two scenarios of climate change.**

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

CONCEPT CHECK 52.2

1. Give examples of human actions that could expand a species' distribution by changing its (a) dispersal or (b) biotic interactions.
2. Explain how the sun's unequal heating of Earth's surface influences global climate patterns.
3. **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 that hypothesis?

For suggested answers, see Appendix A.

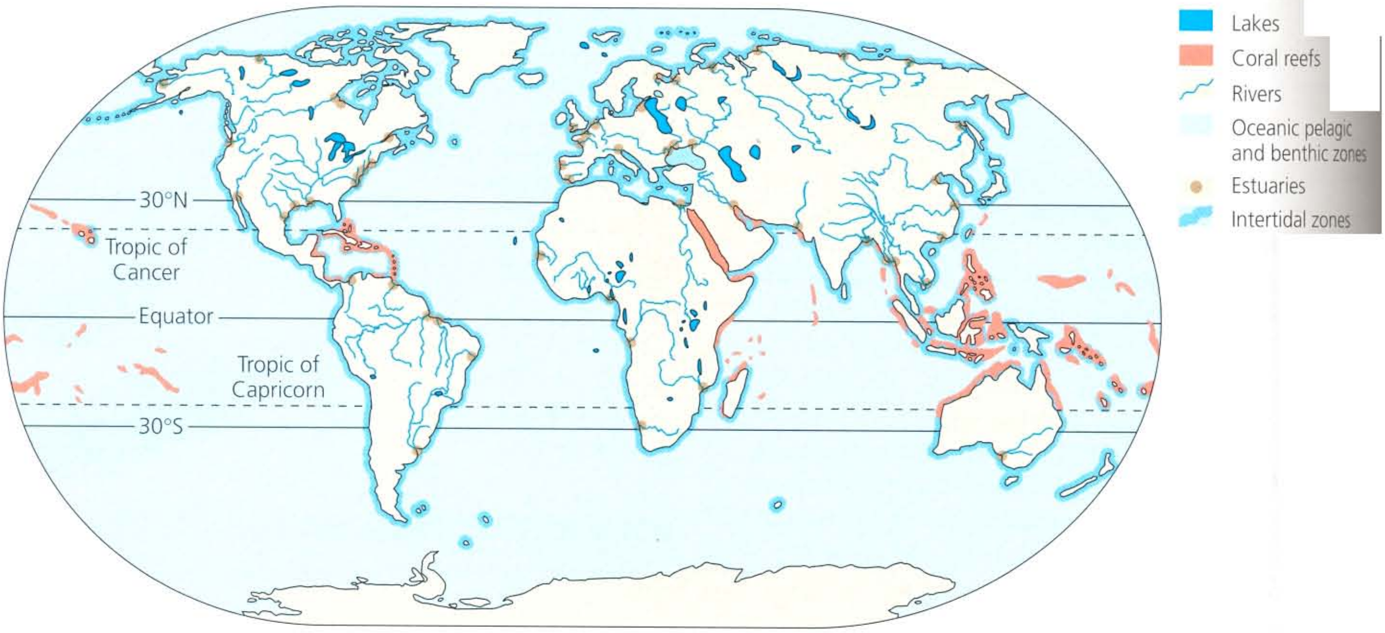
CONCEPT 52.3

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

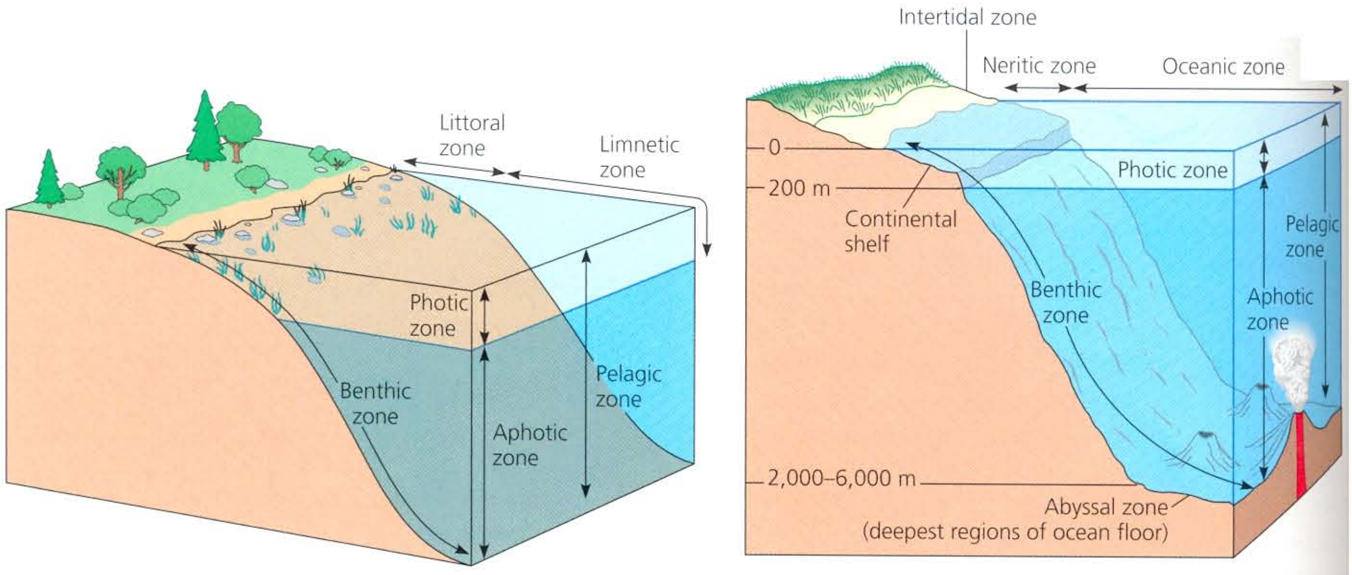
We have seen how both biotic and abiotic factors influence the distribution of organisms on Earth. Combinations of these factors determine the nature of Earth's many **biomes**, major terrestrial or aquatic life zones, characterized by vegetation type in terrestrial biomes or the physical environment in aquatic biomes. We'll begin by examining Earth's aquatic biomes.

Aquatic biomes account for the largest part of the biosphere in terms of area, and all types are found around the globe **(Figure 52.15)**. Ecologists distinguish between freshwater biomes and marine biomes on the basis of physical and chemical differences. For example, 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 have an enormous impact on the biosphere. The evaporation of water from the oceans provides most of the planet's rainfall, and ocean temperatures have a major effect on world climate and wind patterns. In addition, marine algae and



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



(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 it 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 it is open water (pelagic zone) or bottom (benthic and abyssal zones).

▲ **Figure 52.16 Zonation in aquatic environments.**

photosynthetic bacteria 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 terrestrial biomes through which they pass or in which they are situated. 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.

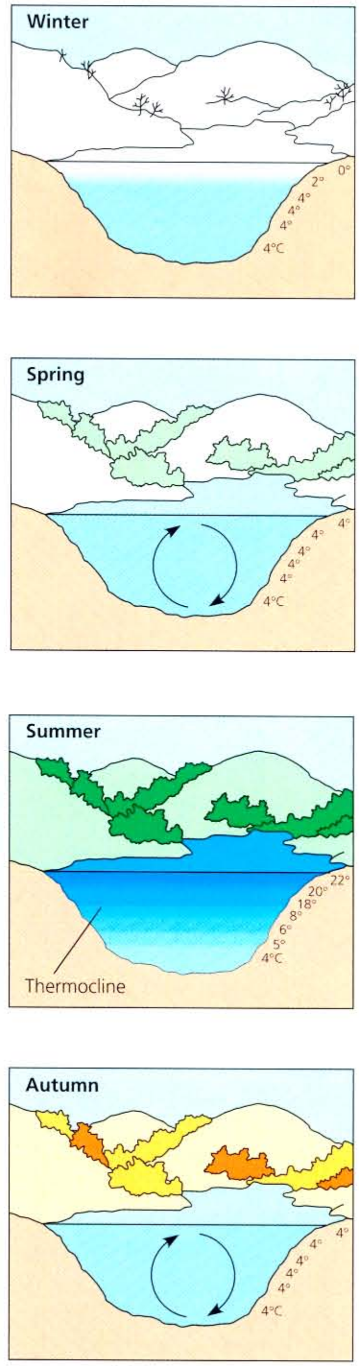
Stratification of Aquatic Biomes

Many aquatic biomes are physically and chemically stratified (layered), as illustrated for both a lake and a marine environment in **Figure 52.16**, on the facing page. Light is absorbed by both the water itself and the photosynthetic organisms in it, so its intensity decreases rapidly with depth, as mentioned earlier. Ecologists distinguish between the upper **photic zone**, where there is sufficient light for photosynthesis, and the lower **aphotic zone**, where little light penetrates. At the bottom of all aquatic biomes, the substrate is called 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. In the ocean, the part of the benthic zone that lies between 2,000 and 6,000 m below the surface is known as the **abyssal 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** 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 profiles **(Figure 52.17)**. This **turnover**, as it is called, brings oxygenated water from a lake's surface to the bottom and 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 52.16b). 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 52.18, on the next four pages, surveys the major aquatic biomes.



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

2 In spring, as the sun melts the ice, the surface water warms to 4°C and sinks below the cooler layers immediately below, eliminating the thermal stratification. Spring winds mix the water to great depth, 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 below the underlying layers, remixing the water until the surface begins to freeze and the winter temperature profile is reestablished.

▲ **Figure 52.17 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 52.18

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 52.16a). Temperate lakes may have a seasonal thermocline (see Figure 52.17); tropical lowland lakes have a thermocline year-round.

An oligotrophic lake in Grand Teton National Park, Wyoming

A eutrophic lake in the Okavango Delta, Botswana

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 ice covered 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 have.

Photosynthetic Organisms Rooted and floating aquatic plants live in the **littoral zone**, the shallow, well-lighted 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 and 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.

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.

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, which in turn support a wide variety of birds. Herbivores, from crustaceans and aquatic insect larvae to muskrats, consume algae, detritus, and plants. Carnivores are also varied and may include dragonflies, otters, alligators, and owls.

Okefenokee National Wetland Reserve in Georgia

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

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 Mississippi River far from its headwaters

Estuaries

estuary in a low coastal plain of Georgia

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 Pollution from upstream, and also filling and dredging, have disrupted estuaries worldwide.

Continued on next page

▼ **Figure 52.18 (continued)**

Exploring Aquatic Biomes

Intertidal Zones

Rocky intertidal zone on the Oregon coast

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.

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 sea grass 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.

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.

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 and renewal of nutrients in temperate oceans produces 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 the 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.

Open ocean off the island of Hawaii

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.

A coral reef in the Red Sea

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.

Marine Benthic Zone

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 52.16b). 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 some areas of organic enrichment, oxygen is present at sufficient concentrations to support a diversity of animals.

A deep-sea hydrothermal vent community

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 52.18.

1. Many organisms living in estuaries experience fresh- and saltwater conditions each day with the rising and falling of tides. What challenge does this pose for the physiology of the organisms?
2. Why are phytoplankton, and not benthic algae or rooted aquatic plants, the dominant photosynthetic organisms of the oceanic pelagic zone?
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**

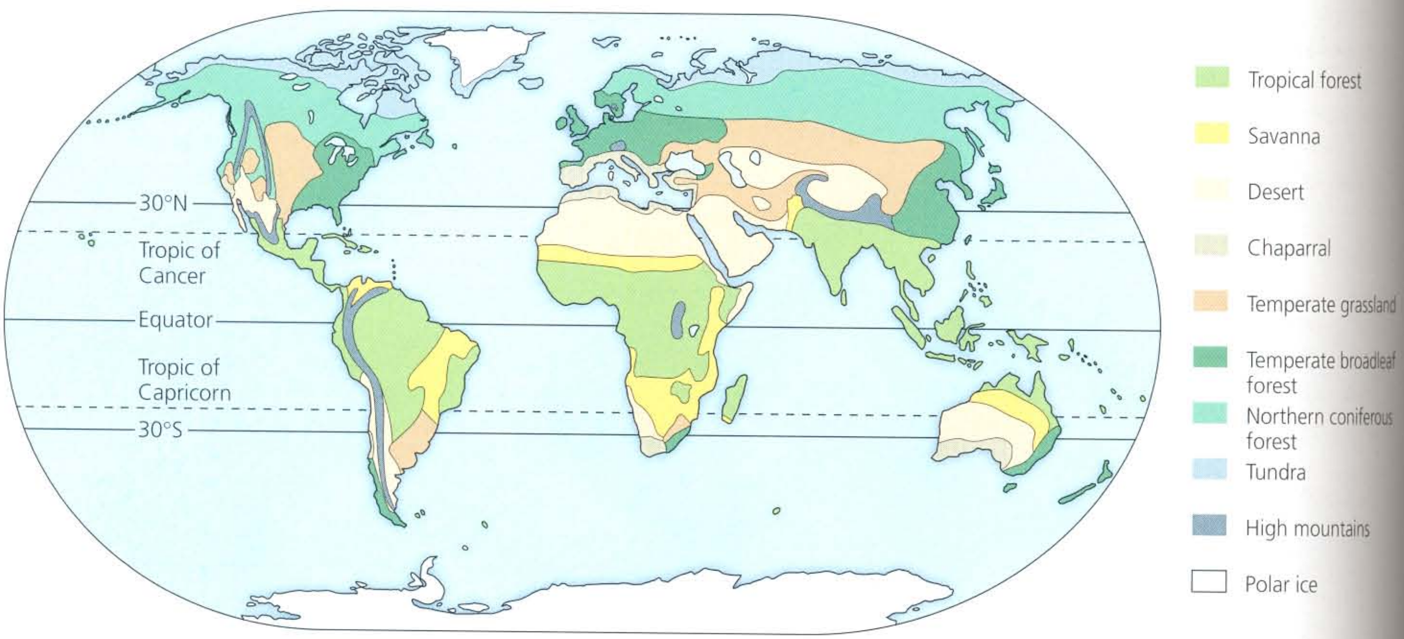
The structure and distribution of terrestrial biomes are controlled by climate and disturbance

All the abiotic factors discussed in this chapter, but especially climate, are important in determining why a particular terrestrial biome is found in a certain area. Because there are latitudinal patterns of climate over Earth's surface (see Figure 52.10), there are also latitudinal patterns of biome distribution **(Figure 52.19)**. These biome patterns in turn are modified by **disturbance**, an event (such as a storm, fire, or human activity) that changes a community, removing organisms from it and altering resource availability. Frequent fires, for instance, can kill woody plants and keep a savanna from becoming the woodland that climate alone would otherwise support.

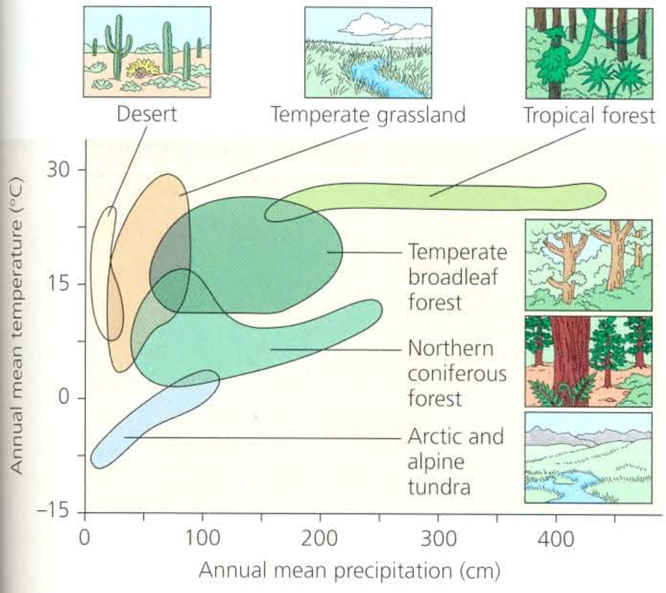
Climate and Terrestrial Biomes

We can see the great impact of climate on the distribution of organisms by constructing a **climograph**, a plot of the temperature and precipitation in a particular region. **Figure 52.20** is a climograph of annual mean temperature and precipitation for some of the biomes found in North America. Notice that the range of precipitation in northern coniferous forests is similar to that in temperate forests, but the temperature ranges are different. Grasslands are generally 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, certain 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. How do 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 with the same annual precipitation have distinct wet and dry seasons. A similar phenomenon may occur with respect to temperature. Other environmental 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 52.19 The distribution of major terrestrial biomes.** Although biomes are mapped here with sharp boundaries, biomes actually grade into one another, sometimes over large areas.



▲ **Figure 52.20 A climograph for some major types of biomes in North America.** The areas plotted here encompass the range of annual mean temperature and precipitation in the biomes.

General Features of Terrestrial Biomes and the Role of Disturbance

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 52.19). Each biome is also characterized by microorganisms, fungi, and animals adapted to that particular environment. For example, temperate grasslands are more likely than forests to be populated by large grazing mammals.

Although Figure 52.19 shows distinct boundaries between the biomes, in actuality, 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, for example, 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 often occupy 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.

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. In an example of convergent evolution (see Figure 26.7), cacti living in North American deserts appear very similar to plants called euphorbs found in African deserts, although cacti and euphorbs belong to different evolutionary lineages.

Biomes are dynamic, and disturbance rather than stability tends to be the rule. For example, hurricanes create openings for new species in tropical and temperate forests. In northern coniferous forests, gaps are produced when old trees die and fall over or when snowfall breaks branches. These gaps allow deciduous species, such as aspen and birch, to grow. As a result, biomes usually exhibit extensive patchiness, with several different communities represented in any particular area.

In many biomes, the dominant plants depend on periodic disturbance. For example, natural wildfires are an integral component of grasslands, savannas, chaparral, and many coniferous forests. However, 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 52.21, 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 original biomes 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.

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

CONCEPT CHECK 52.4

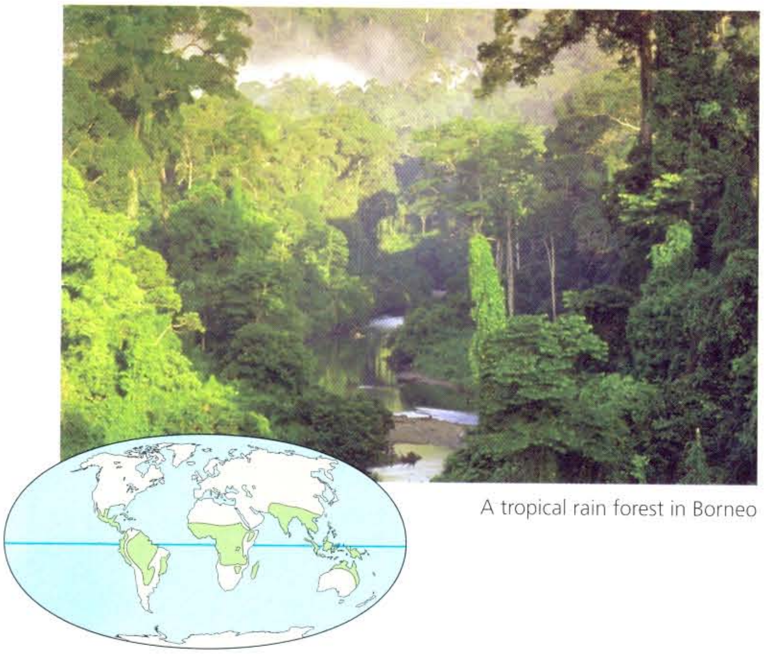
1. Based on the climograph in Figure 52.20, what mainly differentiates dry tundra and deserts?
2. Identify the natural biome in which you live and summarize its abiotic and biotic characteristics. Do these reflect your actual surroundings? Explain.
3. **WHAT IF?** If global warming increases average 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 52.21**

Exploring Terrestrial Biomes

Tropical Forest



A tropical rain forest in Borneo

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.

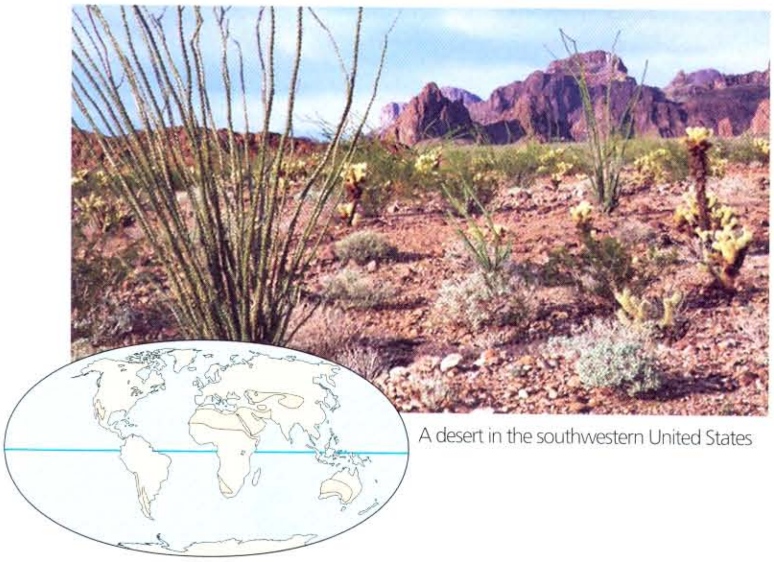
Temperature Air temperatures are high year-round, averaging 25–29°C with little seasonal variation.

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 shrub and herb layers. There are generally fewer layers in tropical dry forests. Broadleaf evergreen trees are dominant in tropical rain forests, whereas 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 some tropical forests.

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, 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 many kinds of 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 on water from metabolic breakdown of carbohydrates in seeds.

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

Savanna

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 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 bison, 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. Cattle ranching and overhunting have led to declines in large-mammal populations.

A savanna in Kenya

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.

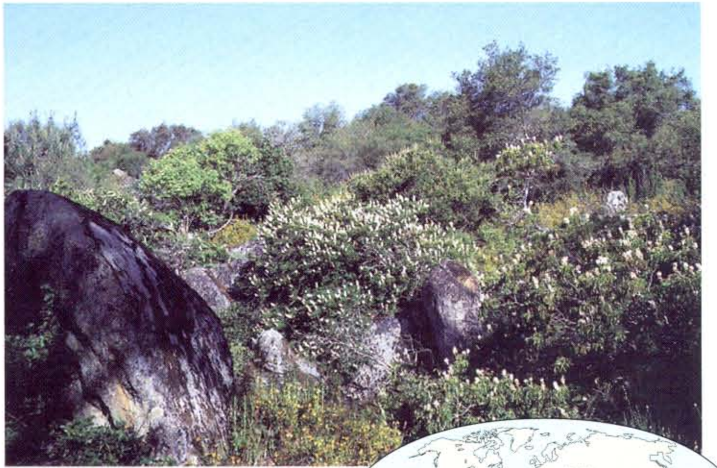
Precipitation Precipitation is highly seasonal, with rainy winters and long, dry summers. Annual precipitation generally falls within the range of 30–50 cm.

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.

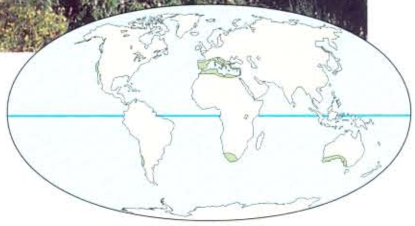
Plants Chaparral is dominated by shrubs and small trees, along with a many kinds of grasses and herbs. Plant diversity is high, with many species confined to a specific, relatively small geographic area. Adaptations to drought include the tough evergreen leaves of woody plants, which reduce water loss. 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



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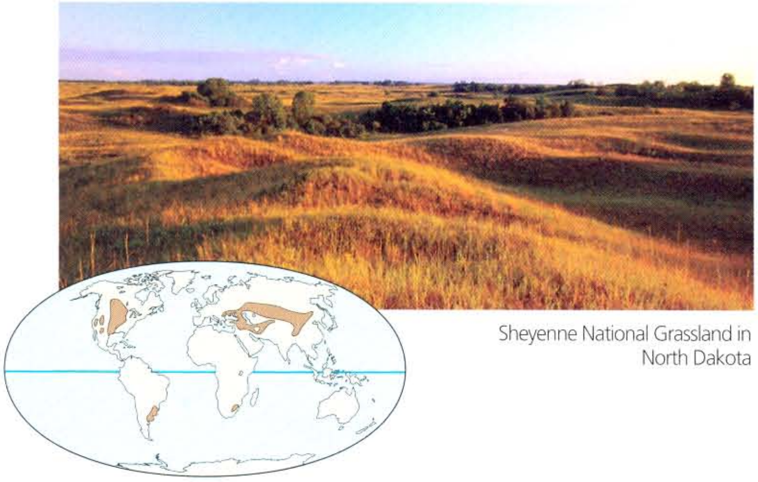
▼ **Figure 52.21 (continued)**

Exploring Terrestrial Biomes

Temperate Grassland



Sheyenne National Grassland in North Dakota

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 all **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.

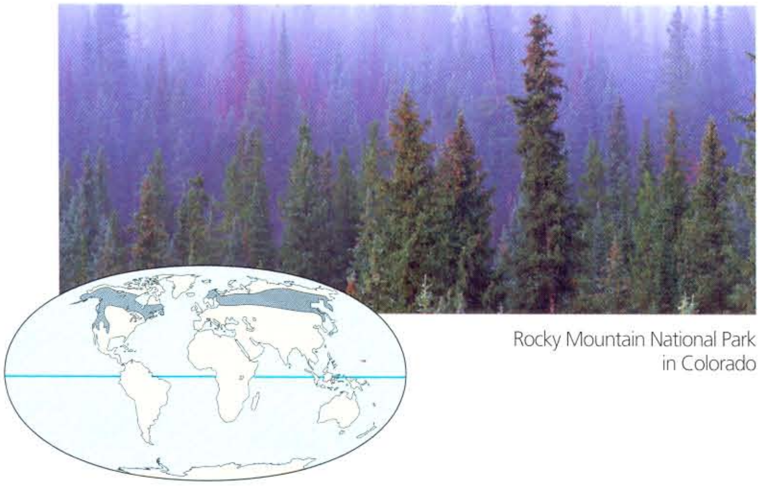
Temperature Winters are generally cold, with average temperatures frequently falling well below −10°C. Summers, with average temperatures often approaching 30°C, are hot.

Plants The dominant plants are grasses and forbs, which vary in height from a few centimeters to 2 m in tallgrass prairie. Many 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 helped change parts of the biome into desert.

Northern Coniferous Forest



Rocky Mountain National Park in Colorado

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 and long; 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 Cone-bearing trees, such as pine, spruce, fir, and hemlock, dominate northern coniferous forests. The conical shape of many conifers prevents too much snow from accumulating and breaking their branches. 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.

Temperate Broadleaf Forest

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

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 herbaceous stratum. 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 dominate these forests.

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

Great Smoky Mountains National Park in North Carolina

Tundra

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

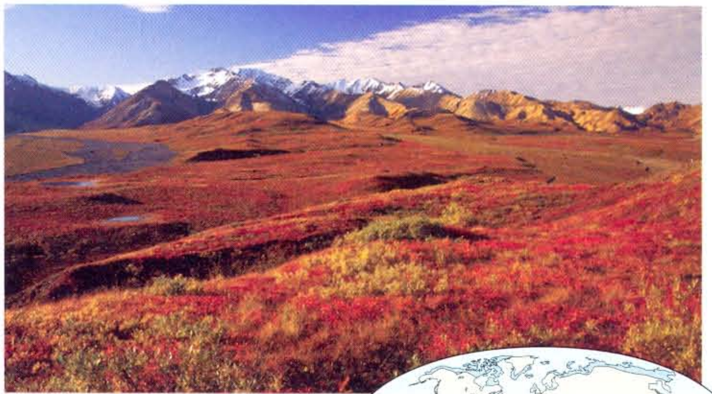
Precipitation Precipitation averages from 20 to 60 cm annually in arctic tundra but may exceed 100 cm in alpine tundra.

Temperature Winters are long and cold, with averages in some areas below −30°C. Summers are short with low temperatures, generally averaging 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

Chapter 52 Review

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SUMMARY OF KEY CONCEPTS

CONCEPT 52.1

Ecology integrates all areas of biological research and informs environmental decision making (pp. 1148–1151)

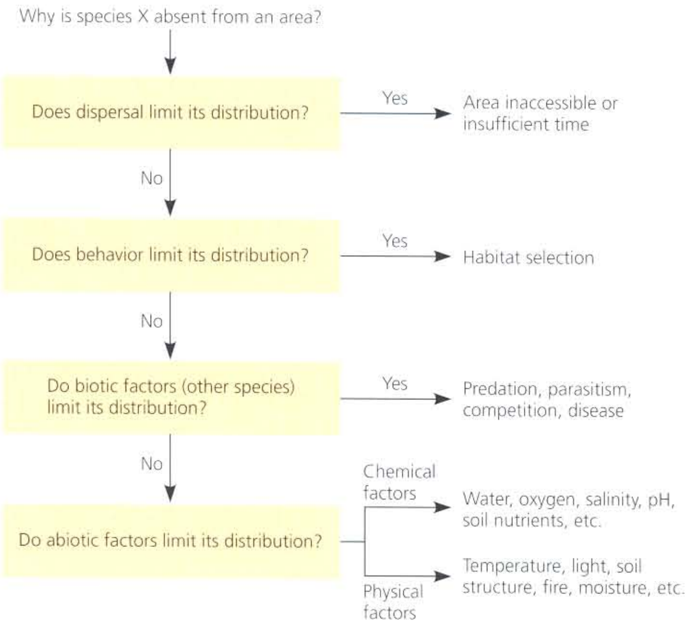
- **Linking Ecology and Evolutionary Biology** Events that occur in ecological time affect life in evolutionary time.
- **Ecology and Environmental Issues** Ecologists distinguish between the science of ecology and environmental advocacy. Ecology provides a scientific basis for solving environmental problems, but policymakers must also balance social, economic, and political factors in reaching their decisions.

MEDIA

Activity Science, Technology, and Society: DDT

CONCEPT 52.2

Interactions between organisms and the environment limit the distribution of species (pp. 1151–1159)



- **Climate** Global climate patterns are largely determined by the input of solar energy and Earth's revolution around the sun. Bodies of water, mountains, and the changing angle of the sun over the year exert regional, local, and seasonal effects on climate. Fine-scale differences in abiotic factors determine microclimates.

MEDIA

Activity Adaptations to Biotic and Abiotic Factors
Investigation How Do Abiotic Factors Affect Distribution of Organisms?

CONCEPT 52.3

Aquatic biomes are diverse and dynamic systems that cover most of Earth (pp. 1159–1166)

- **Stratification of Aquatic Biomes** Aquatic biomes account for the largest part of the biosphere in terms of area and are generally stratified (layered) with regard to light penetration, temperature, and community structure. Marine biomes have a higher salt concentration than freshwater biomes.

MEDIA

Activity Aquatic Biomes

CONCEPT 52.4

The structure and distribution of terrestrial biomes are controlled by climate and disturbance (pp. 1166–1171)

- **Climate and Terrestrial Biomes** Climographs show that temperature and precipitation are correlated with biomes, but because biomes overlap, other abiotic factors play a role in biome location.
- **General Features of Terrestrial Biomes and the Role of Disturbance** 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.

MEDIA

Activity Terrestrial Biomes

TESTING YOUR KNOWLEDGE

SELF-QUIZ

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. WHAT IF? If Earth's axis of rotation suddenly became perpendicular to the plane of its orbit, the most predictable effect would be
   a. no more night and day.
   b. a big change in the length of the year.
   c. a cooling of the equator.
   d. a loss of seasonal variation at high latitudes.
   e. the elimination of ocean currents.

3. 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.

4. 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.

5. 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

6. 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.

7. 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 stratification
   e. cold winter months

8. 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

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

10. **DRAW IT** After reading the experiment of W. J. Fletcher described in Figure 52.8, 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

For Self-Quiz answers, see Appendix A.

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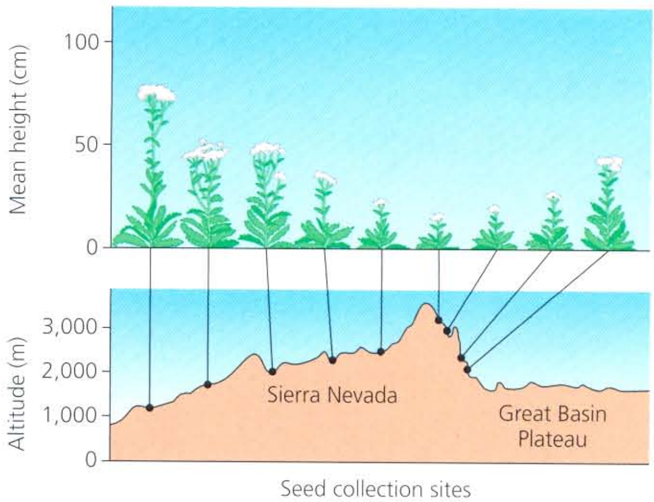
EVOLUTION CONNECTION

11. 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?

SCIENTIFIC INQUIRY

12. 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?