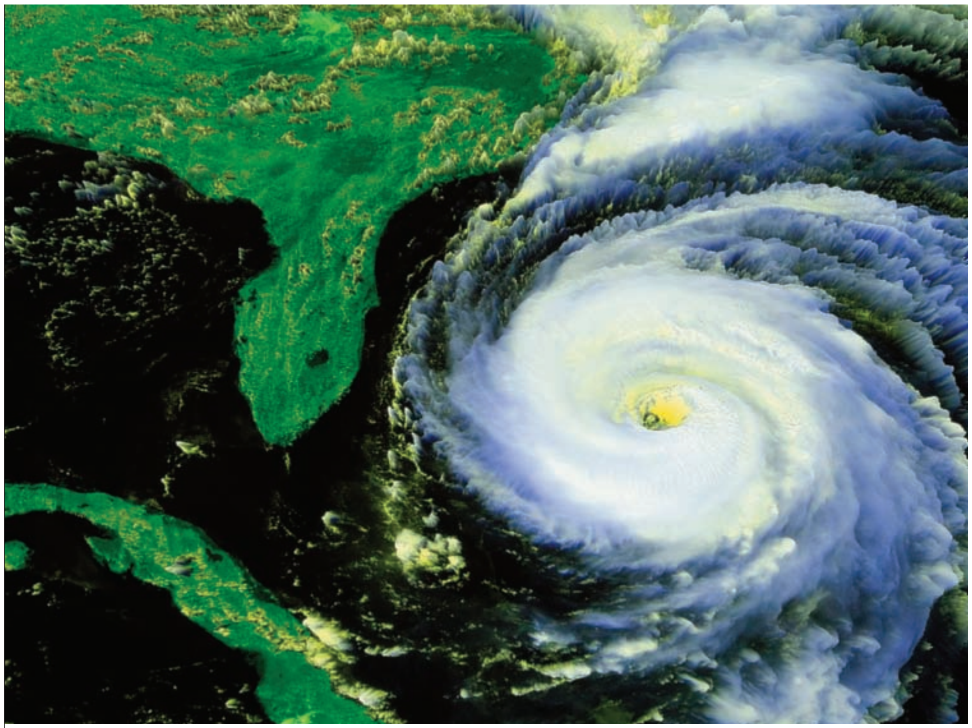
Stormy weather in the biosphere. Atmospheric disturbances like Hurricane Fran, seen here in a satellite photograph taken on September 4, 1996, often have a dramatic impact on living systems.



NOAA/Photo Researchers, Inc.

## Study Plan



# 52 The Biosphere

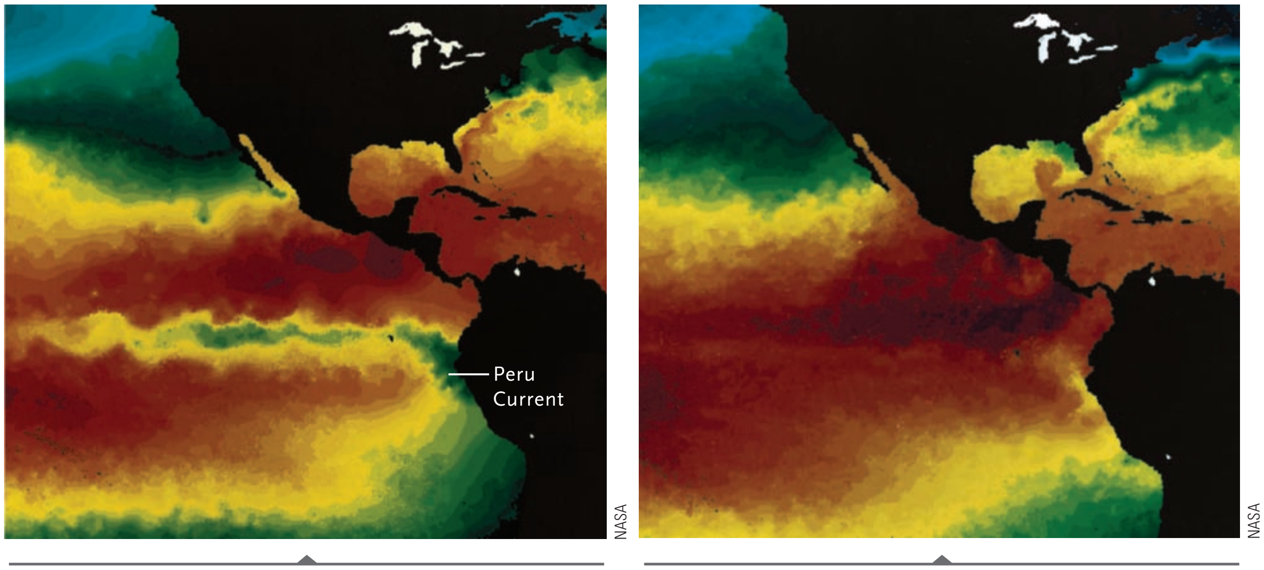
## Why It Matters

The winter of 1997–1998 was one for the books. Record rainfall caused mudslides in California and flooding along the normally arid coast of Ecuador and Peru. But the annual rains never arrived in Asia and Australia, and fires consumed tropical rain forests in Indonesia and Malaysia. What caused these major climatic dislocations? Every 3 to 7 years, interactions between the upper layers of the Pacific Ocean and the atmosphere produce El Niño, a climatic event with global consequences **(Figure 52.1).** The 1997–1998 El Niño altered weather patterns worldwide, killing more than 2000 people and causing at least $30 billion in property damage.

In most years, air flows from a high pressure system over the eastern Pacific toward a low pressure system over the western Pacific. These winds move surface water from east to west and bring heavy rains to parts of Asia and Australia. Winds also usually blow from the poles toward the equator along the western sides of continents, and Earth's rotation causes these winds to push ocean surface water westward, away from the coast. The displaced surface water is replaced by cold, deep, nutrient-rich water carried by vertical currents called *upwellings* (see Figure 52.1a). The nutrients support complex marine

**a.** Usual pattern of Pacific Ocean currents

**b.** Pacific Ocean currents in an El Niño year




In most years, the powerful Peru Current carries cold water from the ocean bottom to the surface off the west coast of South America. The cold surface water then flows westward along the equator toward a large pool of warm water in the western Pacific Ocean. In this satellite photo taken on May 31, 1988, dark red indicates the warmest water and dark green the coldest upwelled water.

During an El Niño event, equatorial winds reverse directions and warm surface water flows eastward along the equator from the western Pacific Ocean toward South America. In this satellite photo taken on May 13, 1992, the warm water (red) spreads up and down the west coast of North and South America, suppressing the upwelling of cold water by the Peru Current.

**Figure 52.1** El Niño and Pacific Ocean currents.

food webs in the shallow water above the continental shelf. For example, the Peru Current along the west coast of South America once supported a rich anchovy fishery.

Ocean currents vary seasonally, however, and in late December or early January, a warm, nutrient-poor current flows eastward along the equator and then north and south along the coastlines of Central and South America. Peruvian fishermen call this warm current El Niño (Spanish for "the child"), because it reaches their coast around Christmas. It usually persists for only a few weeks.

In strong El Niño years, atmospheric pressure systems change over the Pacific, altering the prevailing winds and ocean currents. Equatorial winds weaken; surface currents reverse direction, flowing from west to east; and a huge pool of warm ocean water accumulates in the eastern Pacific. During these shifts, the heavy rain that usually falls on Asia and Australia is instead delivered to the central and eastern Pacific. Thus, in El Niño years, Asia and Australia receive less rain than usual, and the west coasts of the Americas receive more. In the United States, winter temperatures are unusually high in the north central states and unusually low in the southern states.

El Niño episodes also alter sea surface temperature. When the warm current flowing from west to east reaches the continental shelf, it displaces the cold water of the Peru Current and prevents the usual upwelling (see Figure 52.1b). These changes in ocean currents have catastrophic effects on marine food webs. Lacking sufficient nutrients, phytoplankton die, followed by fishes that eat phytoplankton, and seabirds that eat fishes. In combination with overfishing, the El Niño of 1972 drove the Peruvian anchovy population to the brink of extinction.

Some El Niño years are followed by a weather pattern called La Niña: the low pressure system over the western Pacific is accentuated, pulling air and ocean surface water from east to west. Low ocean surface temperatures extend from the coast of South America to Samoa. La Niña's effect on winter weather is opposite that of El Niño: parts of Asia and Australia are unusually wet; and the northern United States experiences periods of cold, wet weather, whereas the southern region is unusually warm and dry.

El Niño and La Niña are two extremes of a global climate cycle called the El Niño Southern Oscillation, or ENSO (the name refers to fluctuations in air pressure over the tropical Pacific). ENSO is a product of large-scale interactions between the ocean and atmosphere and has a major impact on the **biosphere**, all the places on Earth where organisms live. The biosphere has three abiotic components, which surround Earth's geological bulk like a skin. The **hydrosphere** encompasses all the water, including oceans and polar ice caps. The **lithosphere** includes the rocks, sediments, and soils of the crust. Finally, the **atmosphere** includes gases and airborne particles that envelop the planet.

In this chapter, we survey the biosphere with a wide-angle lens. First, we examine its environmental diversity and how organisms cope with it. We then consider how variations in the physical environment influence the large-scale distributions of ecosystems on land, in fresh water, and in the sea.

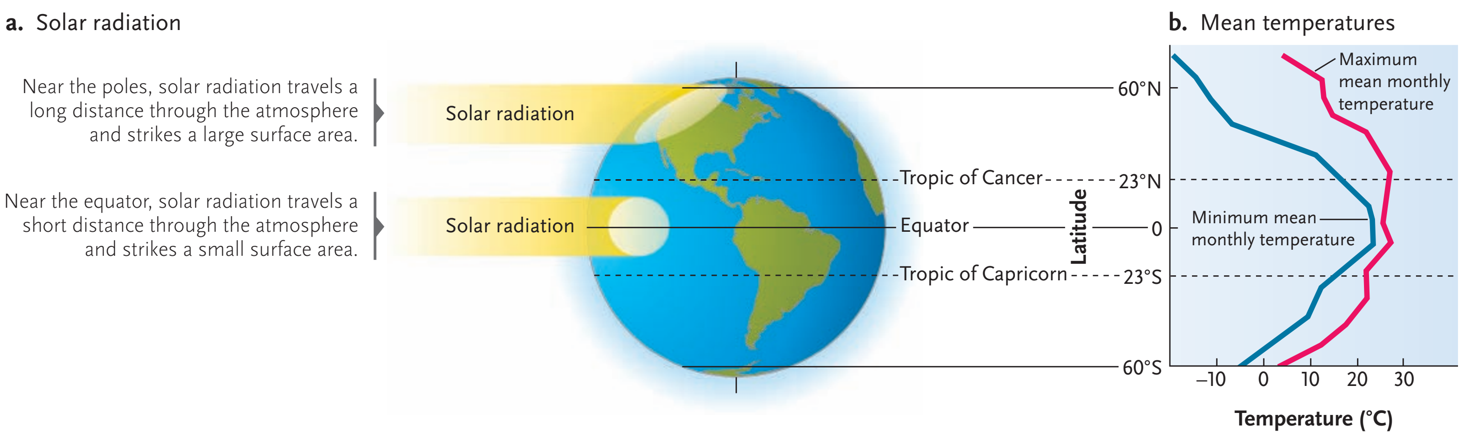



**Figure 52.2**
**Latitudinal variation in solar radiation and temperature. (a)** Solar radiation is more intense near the equator than near the poles. **(b)** Minimum and maximum mean monthly temperatures as well as the range of mean monthly temperatures vary with latitude.

## 52.1 Environmental Diversity of the Biosphere

Numerous abiotic factors—sunlight, temperature, humidity, wind speed, cloud cover, and rainfall—contribute to a region's **climate,** the weather conditions prevailing over an extended period of time. Climates vary on global, regional, and local scales, and they undergo seasonal changes almost everywhere.

### Variations in Incoming Solar Radiation Create Global Climate Patterns

A global pattern of environmental diversity results from latitudinal variation in incoming solar radiation, Earth's rotation on its axis, and its orbit around the sun.

**Solar Radiation.** Earth's spherical shape causes the intensity of incoming solar radiation to vary from the equator to the poles **(Figure 52.2).** When sunlight strikes Earth directly at a 90° angle, as it does near the equator, it travels the shortest possible distance through the radiation-absorbing atmosphere and falls on the smallest possible surface area (see Figure 52.2a). When sunlight arrives at an oblique angle, as it does near the poles, it travels a longer distance through the atmosphere and shines on a larger area. Thus, solar radiation is more concentrated near the equator than it is at higher latitudes, causing latitudinal variation in temperature (see Figure 52.2b).

**Seasonality.** Earth is tilted on its axis at a fixed position of 23.5° from the perpendicular to the plane on which it orbits the sun **(Figure 52.3).** This tilt produces seasonal variation in the duration and intensity of incoming solar radiation. The Northern Hemisphere receives its maximum illumination—and the Southern Hemisphere its minimum—on the June solstice (around June 22), when the sun shines directly over the Tropic of Cancer (23.5° N latitude). The reverse is true on the December solstice (around December 22), when the sun shines directly over the Tropic of Capricorn (23.5° S latitude). Twice each year, on the vernal and autumnal equinoxes (around March 21 and September 23, respectively), the sun shines directly over the equator.

Earth's tilt is permanent, and only the **tropics**—the latitudes between the Tropics of Cancer and Capricorn—ever receive intense solar radiation from directly overhead. Moreover, the tropics experience only small seasonal changes in temperature and day length: environmental temperature is high and days last approximately 12 hours throughout the year. (Tropical seasonality is reflected in the alternation of wet and dry periods, rather than warm and cold seasons.) Seasonal variation in temperature and day length increases steadily toward the poles. Polar winters are long and cold with periods of continuous dark-

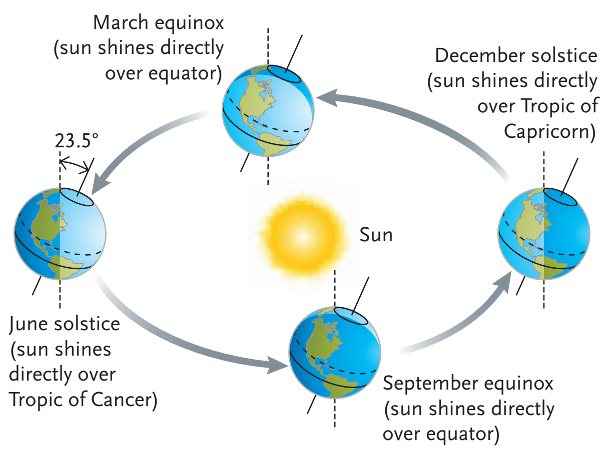



**Figure 52.3**
**Seasonal variation in solar radiation.** Earth's fixed tilt on its axis causes the Northern Hemisphere to receive more sunlight in June and the Southern Hemisphere to receive more in December. These differences are reflected in seasonal variations in day length and temperature, which are more pronounced at the poles than at the equator.

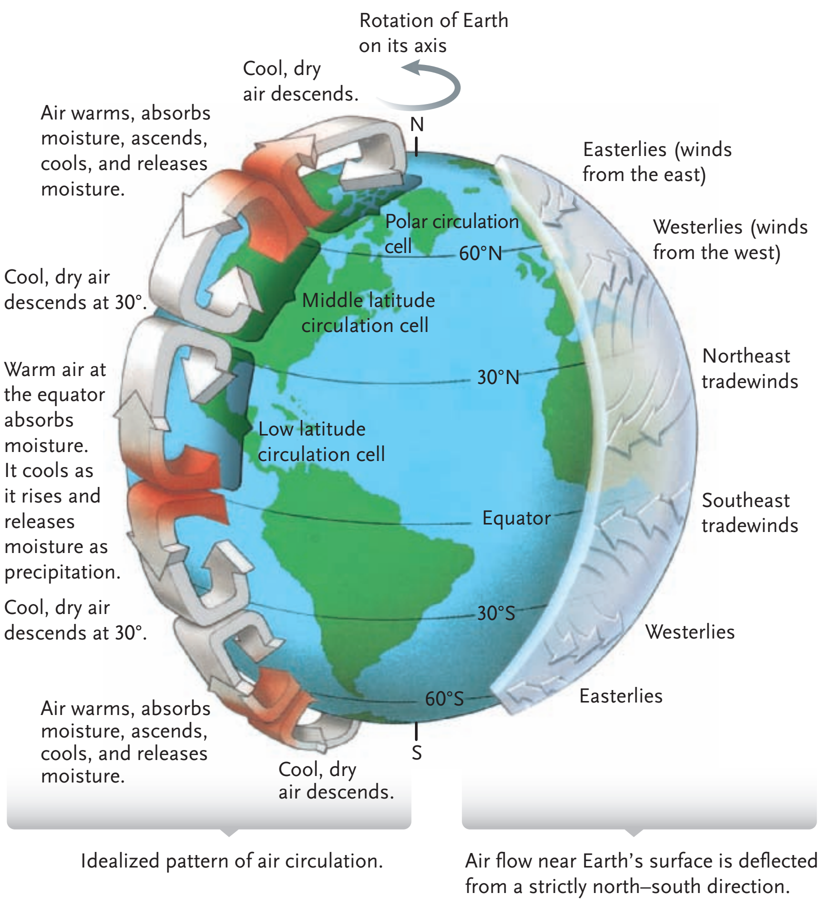



**Figure 52.4**
Global air circulation. Latitudinal variations in the intensity of solar radiation cause equatorial air masses to warm and rise, initiating a global pattern of air movement in three circulation cells in each hemisphere. Air masses moving near Earth's surface create easterly and westerly winds, which are deflected from a strictly north–south flow by the planet's rotation.

ness, and polar summers are short with periods of continuous light.

**Air Circulation.** Sunlight warms air masses, causing them to expand, lose pressure, and rise in the atmosphere. The unequal heating of air at different latitudes initiates global air movements, producing three circulation cells in each hemisphere **(Figure 52.4).** Warm equatorial air masses rise to high altitude before spreading north and south. They eventually sink back to Earth at about 30° N and S latitude. At low altitude, some air masses flow back toward the equator, completing low-latitude circulation cells. Others flow toward the poles, rise at 60° latitude, and divide at high altitude. Some air flows toward the equator, completing the pair of middle-latitude circulation cells. The rest moves toward the poles, where it descends and flows toward the equator, forming the polar circulation cells.

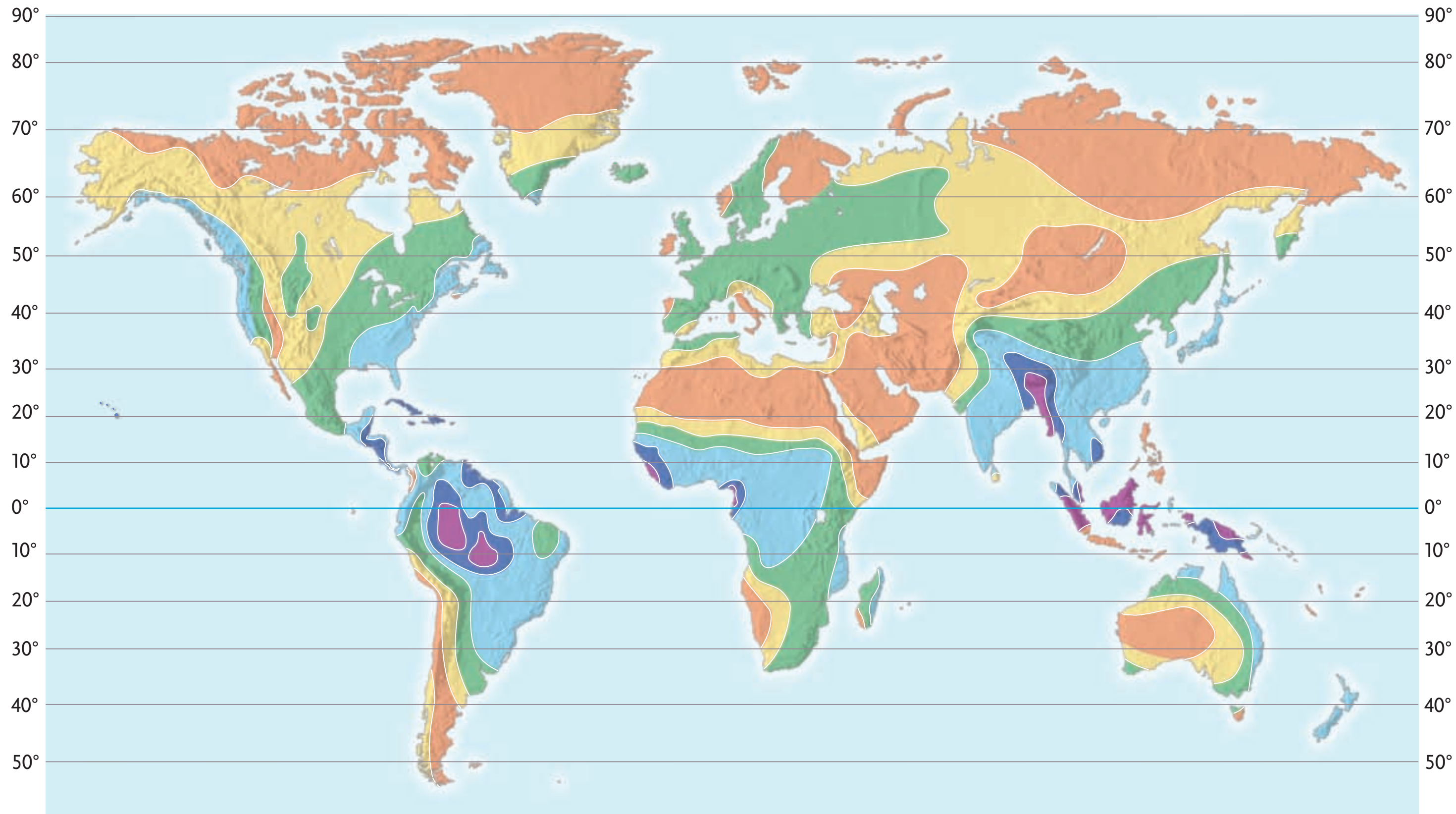
The flow of air masses at low altitude creates winds near the planet's surface. But the surface rotates beneath the atmosphere, moving rapidly near the equator, where Earth's diameter is greatest, and slowly near the poles. Latitudinal variation in the speed of rotation deflects the movement of the rising and sinking air masses from a strictly north–south path into belts of easterly and westerly winds (see Figure 52.4); this deflection is called the Coriolis effect. Winds near the equator are called the trade winds; those further from the equator are the temperate westerlies and easterlies, named for the direction from which they blow.

**Precipitation.** Differences in solar radiation and global air circulation create latitudinal variations in rainfall **(Figure 52.5).** Warm air holds more water vapor than cool air does. As air near the equator heats up, it absorbs water, primarily from the oceans. However, the warm air masses expand as they rise, and their heat energy is distributed over a larger volume, causing their temperature to drop. A decrease in temperature without the actual *loss* of heat energy is called **adiabatic cooling.** After cooling adiabatically, the rising air masses release moisture as rain. Torrential rainfall is characteristic of warm equatorial regions, where rising, moisture-laden air masses cool as they reach high altitude.

As cool, dry air masses descend at 30° latitude, increased air pressure at low altitude compresses them, concentrating their heat energy, raising their temperature, and increasing their capacity to hold moisture. The descending air masses absorb water from the land, so these latitudes are typically dry. Some air masses continue moving poleward in the lower atmosphere. When they rise at 60° latitude, they cool adiabatically and release precipitation (see Figure 52.4), creating moist habitats in the northern and southern temperate zones.

**Ocean Currents.** Latitudinal variations in solar radiation also warm the oceans' surface water unevenly. Because the volume of water increases as it warms, sea level is about 8 cm higher at the equator than at the poles. The volume of water associated with this "slope" is enough to cause surface water to move in response to gravity. The trade winds and temperate westerlies also contribute to the mass flow of water at the ocean surface. Thus, surface water flows in the direction of prevailing winds, forming major currents. Earth's rotation, the positions of landmasses, and the shapes of ocean basins also influence their movement.

Oceanic circulation is generally clockwise in the Northern Hemisphere and counterclockwise in the Southern **(Figure 52.6).** The trade winds push surface water toward the equator and westward until it contacts the eastern edge of a continent. Swift, narrow, and deep currents of warm, nutrient-poor water run toward the poles, parallel to the east coasts of continents. For ex-

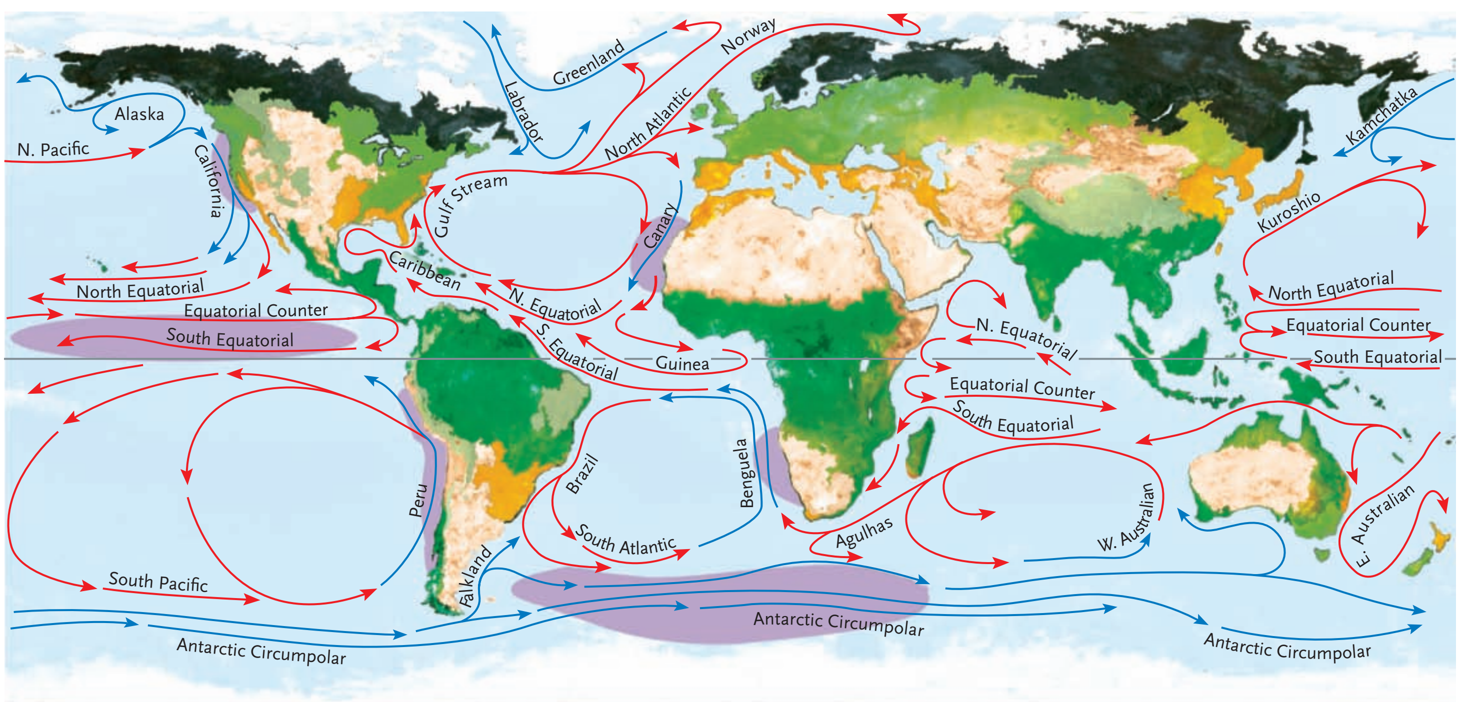



KEY

**Precipitation (cm)**

- Under 25
- 25 to 50
- 50 to 100
- 100 to 200
- 200 to 250
- Over 250

**Figure 52.5**
**Variations in precipitation.** The tropics receive high annual rainfall, whereas regions near 30° latitude are usually dry. Local topographic features and ocean currents also influence precipitation patterns.




KEY

- Upwelling zone
- Warm surface current
- Cold surface current

**Figure 52.6**
**Ocean currents.** Prevailing winds, Earth's rotation, gravity, the shape of ocean basins, and the positions of landmasses establish the direction and intensity of surface currents in the oceans. In general, warm currents flow away from the equator, and cold currents flow toward it.

ample, the Gulf Stream flows northward along the east coast of North America, carrying warm water toward northwestern Europe. Cold water returns from the poles toward the equator in slow, broad, and shallow currents, such as the California Current, that parallel the west coasts of continents.

## Regional and Local Effects Overlay Global Climate Patterns

Although global and seasonal patterns determine a site's climate, regional and local effects also influence abiotic conditions.

**Proximity to the Ocean.** Currents running along seacoasts exchange heat with air masses flowing above them, moderating the temperature over nearby land. Breezes often blow from the sea toward the land during the day and in the opposite direction at night **(Figure 52.7).** These local effects sometimes override latitudinal variations in temperature. For example, the climate in London is much milder than that in Minneapolis, even though Minneapolis is slightly further south. Minneapolis has a **continental climate** that is not moderated by the distant ocean, but London has a **maritime climate,** tempered by winds that cross the nearby North Atlantic Current.

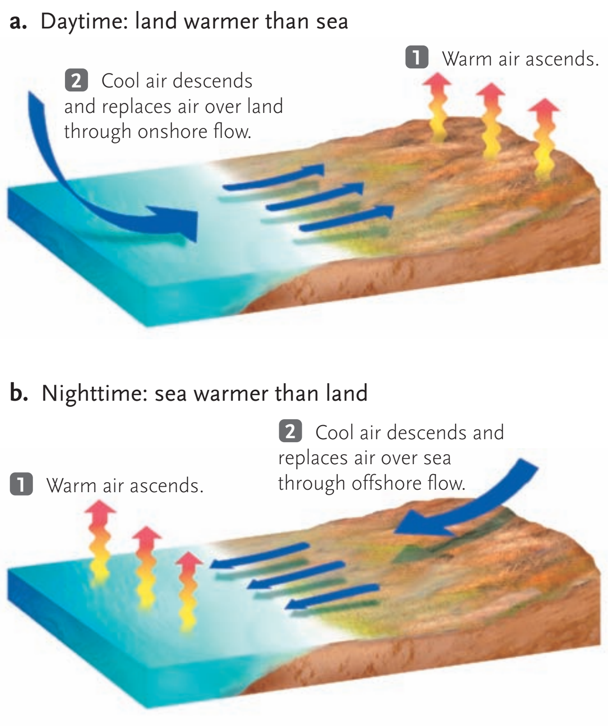



**Figure 52.7**
Sea breezes and land breezes. On a summer afternoon **(a),** warm air rises over the land, and a cool sea breeze blows inland from the ocean. At night **(b),** when the ocean is warmer than the land, the pattern is reversed.

Ocean currents also affect moisture conditions in coastal habitats. For example, air masses absorb water as they move from west to east across the Pacific Ocean. They cool as they cross the cold California Current, and when they reach land in northern California and Oregon during winter, their water vapor condenses into heavy fog and rain. During summer, however, land is warmer than the adjacent ocean. The air masses heat up as they cross the land, and they accumulate water, creating dry conditions.

Some regions experience **monsoon cycles** caused by seasonal reversals of wind direction. In the North American southwest, for example, summer heat causes air masses over land to rise, creating a zone of low pressure. Moist air from the nearby Gulf of California flows inland, where it rises and cools adiabatically, releasing substantial precipitation. Summer monsoon rains deliver one-third to one-half of the annual rainfall in Arizona and New Mexico. During the winter, when land is cooler than the nearby ocean, low-pressure systems form over the ocean, and winds blow from the land to the sea; thus, winters in the southwest are generally dry. Seasonal monsoon cycles also deliver torrential rainfall to parts of Africa, Asia, and South America.

**The Effects of Topography.** Mountains, valleys, and other topographic features also influence regional climates. In the Northern Hemisphere, south-facing slopes are warmer and drier than north-facing slopes, because they receive more solar radiation. In addition, adiabatic cooling causes air temperature to decline 3° to 6°C for every 1000 m increase in altitude.

Mountains also establish regional and local rainfall patterns. For example, after a warm air mass picks up moisture from the Pacific Ocean, it moves inland and reaches the Sierra Nevada, which parallels the California coast. As it rises to cross the mountains, the air cools adiabatically and loses moisture, releasing heavy rainfall on the windward side **(Figure 52.8).** After the now-dry air crosses the peaks, it descends and warms, absorbing moisture and forming a **rain shadow.** Habitats on the leeward side of mountains, such as the Great Basin Desert in western North America, are typically drier than those on the windward side.

**Microclimate.** Although climate influences the overall distributions of organisms, the abiotic conditions that immediately surround them—the **microclimate**—have the greatest effect on survival and reproduction. For example, a fallen log on the forest floor creates a microclimate in the underlying soil that is shadier, cooler, and moister than surrounding soil exposed to sun and wind. Many animals, including some insects, worms, salamanders, and snakes, occupy these sheltered sites and avoid the effects of prolonged exposure to the elements.

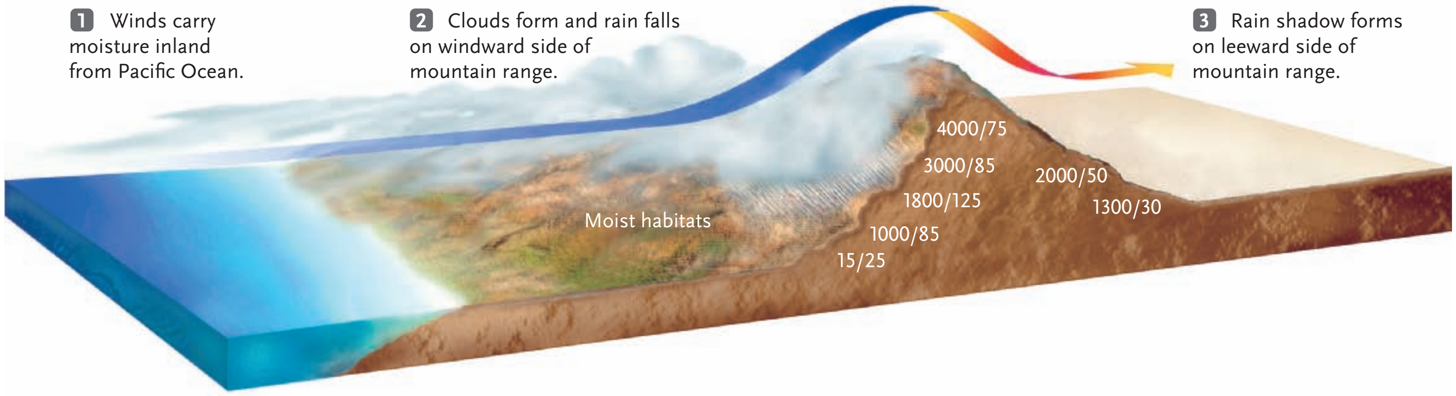



**Figure 52.8** Formation of a rain shadow. White numbers indicate altitude in meters followed by mean annual precipitation in centimeters for the Sierra Nevada of California.

### Study Break

1. How does Earth's spherical shape influence temperature and air movements at different latitudes?
2. What causes seasonality of the climate in the temperate zone?
3. Why do dry conditions occur at 30° N and S latitude?
4. Briefly describe how mountains influence local precipitation.

## 52.2 Organismal Responses to Environmental Variation

Daily and seasonal variations in physical factors have profound effects on the biology of individual organisms. Moreover, large-scale variations in environmental conditions often influence the distributions of populations.

### Organisms Use Homeostatic Responses to Cope with Environmental Variation

Animals in particular exhibit diverse homeostatic responses—biochemical, behavioral, physiological, and morphological—that enable them to maintain relatively constant conditions within their cells and tissues. Although the ability to use these responses almost certainly has a genetic basis, only some responses to environmental variation are *obligate* (that is, they must always be used). *Insights from the Molecular Revolution* describes one such evolutionary response at the biochemical level. Many behavioral and physiological responses are *facultative*. In other words, animals may use them or not, as their immediate conditions demand. Here we provide two brief examples of facultative behavioral and physiological responses to variations in environmental temperature.

Like many ectothermic animals, lizards often use behaviors to regulate body temperature (see Figure 1.15 and Section 46.6). They commonly *bask* in sunny spots to raise body temperature and seek shaded places to cool off. Many *Anolis* lizard species (see *Focus on Research Organisms* in Chapter 30) are distributed over broad altitudinal ranges, and populations living at high altitude encounter cooler environments than do those at low altitude. While they were graduate students at Harvard University, Paul E. Hertz, now of Barnard College, and Raymond B. Huey, now of the University of Washington, hypothesized that *Anolis* populations living at cool, high altitudes would bask more frequently than those living at warm, low altitudes. Hertz and Huey tested their hypothesis by observing *Anolis cybotes* and its close relative *Anolis shrevei* along an altitudinal gradient in the Dominican Republic **(Figure 52.9).** Their results indicate that basking frequency increases steadily with altitude. Moreover, the body temperatures of the lizards vary much less with altitude than do air temperatures at the same localities. The researchers therefore concluded that increased basking frequency by lizards at high altitude partially compensates for the lower environmental temperatures they encounter.

The state of extreme physiological sluggishness called *torpor* is a facultative response to daily variations in environmental temperature. Endothermic animals use the heat generated by the metabolic breakdown of food to maintain high body temperature (see Section 46.6). However, small endotherms, such as hummingbirds, have a large relative surface area through which they lose body heat. When environmental temperature is low, they may lose heat faster than they can generate it, risking the total depletion of their energy reserves and death by starvation. The problem is particularly acute at night, when hummingbirds cannot feed to replenish their energy stores. F. Reed Hainsworth and Larry Wolf of Syracuse University discovered that the purple-throated carib *(Eulampis jugularis)*, a West Indian hummingbird, often becomes torpid at night, lowering its body

## Insights from the Molecular Revolution

### Fish Antifreeze Proteins

Polar-dwelling fishes, such as winter flounder, Alaskan plaice, and Arctic sculpin, have "antifreeze proteins" that prevent their bodies from freezing into solid ice at the extremely low environmental temperatures they encounter. As ice crystals begin to form within a fish's cells and tissues, the antifreeze proteins bind to the crystals and cover them with a protein coat that prevents further crystal growth and fusion. As a result, the fishes freeze only to an ultrafine slush that allows continued activity, including movement and feeding. The antifreeze proteins are small molecules containing between 30 and 50 amino acids.

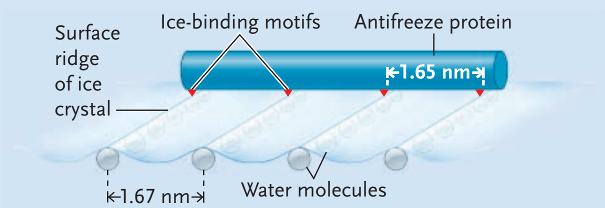



**Figure a**
How winter flounder antifreeze protein may bind to the surface ridges of an ice crystal. Only the water molecules forming the tips of the ridges are shown.

Researchers do not fully understand how the antifreeze proteins bind to ice crystals. Frank Sicheri and D. S. C. Yang at McMaster University in Hamilton, Ontario, and the Bio-Crystallography Laboratory of the VA Medical Center in Pittsburgh, Pennsylvania, sought a molecular solution to this problem. They used X-ray diffraction (see Section 14.2) to work out the molecular structure of the antifreeze protein from the winter flounder *(Pseudopleuronectes americanus)*. They grew protein crystals in a solution at 4°C and then examined them by X-ray diffraction at 4°C and −180°C.

The X-ray diffraction data indicated that the 37 amino acids of the antifreeze protein wind into a single, linear alpha helix. Along one side of the helix, side groups of two polar amino acids, threonine and asparagine, extend from the surface at four evenly spaced locations in a flat plane, one at either end of the molecule and two within the helix. Sicheri and Yang propose that these locations, which are spaced 1.65 nm apart, are *ice-binding motifs*. The four motifs would fit nicely to the tips of ridges formed by water molecules on the surface of an ice crystal, which are spaced at intervals of 1.67 nm **(Figure a).** Hydrogen bonds between the polar amino acid side groups and water molecules along the ridges would hold the proteins tightly to the surface of the ice crystal. The tight fit would prevent more water molecules from adding to the ice surface and thereby prevent further crystal growth.

Understanding how the fish antifreeze proteins work is not just a fascinating scientific issue. The description and characterization of the antifreeze proteins could lead to medical and industrial applications in situations where procedures and equipment must tolerate freezing conditions. In fact, the U.S. Food and Drug Administration recently approved the use of an antifreeze protein—originally discovered in an arctic fish, but now produced by genetically engineered yeast—as an ingredient in ice cream to enhance its creamy texture.

temperature from 40° to 20°C. Because torpor reduces the temperature difference between their bodies and the environment, torpid birds lose heat less rapidly. At the nighttime environmental temperatures they usually encounter, the torpid hummingbirds may use 80% less energy than they would if they had not entered a temporarily dormant state.

## Global Warming Is Changing the Ecology of Many Organisms

As described in Chapter 51's *Focus on Applied Research,* most scientists agree that the atmosphere is getting warmer. What effect will global warming have on biological systems? Biologists hypothesize that, on the spatial scale of the biosphere, rising temperatures will affect the geographical distributions of populations, species, and communities. Models of climate change predict that the distributions of polar species will contract to even higher latitudes, and the ranges of temperate and tropical species will expand or shift toward the poles. The models also predict that global warming will change the timing of important biological events. For example, plants whose flowering is triggered by warm springtime temperatures will flower earlier in the season; similarly, migratory animals will return from their wintering grounds and begin reproducing earlier in the year.

Camille Parmesan of the University of Texas at Austin and Gary Yohe of Wesleyan University tested these predictions with a massive literature review. They surveyed studies of changes in the geographical distributions and timing of springtime activities in a wide variety of herbaceous plants, trees, invertebrates, and vertebrates over roughly the past 100 years. Their analysis, published in 2003, suggests that the geographical ranges of 99 species of butterflies, birds, and alpine herbs in the Northern Hemisphere have shifted dramatically into habitats that had previously been too cold for them. Some species have expanded their distributions northward an average of 6.1 km per decade. Other species have shifted their distributions to higher altitude, an average of 6.1 m per decade. Their analysis also indicated that for 172 species of plants, butterflies, amphibians, and birds, springtime growth and reproduction has occurred on average 2.3 days earlier per decade. If these trends continue at the same rate, spring flowering and animal reproduction will occur

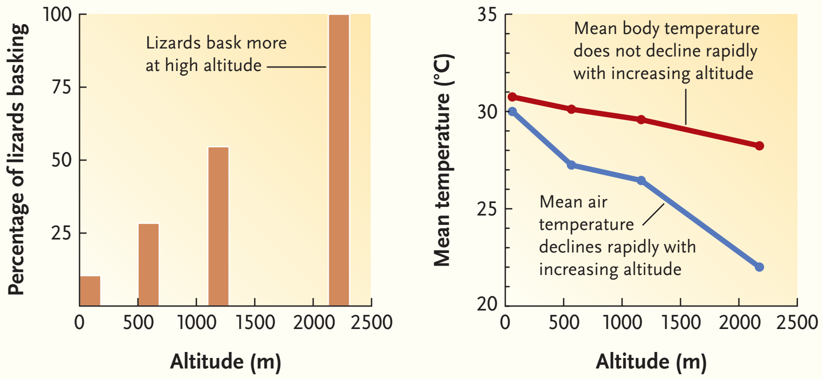
## Figure 52.9 Observational Research

### *How Lizards Compensate for Altitudinal Variations in Environmental Temperature*

**HYPOTHESIS:** Lizards living at high altitude can use behaviors to compensate for the low environmental temperatures they encounter.

**PREDICTION:** The percentage of lizards observed basking in the sun will increase with altitude, and mean air temperatures will vary more than lizard body temperatures among study sites distributed along an altitudinal gradient.

**METHOD:** Hertz and Huey measured the basking behavior as well as air temperatures and body temperatures of two closely related species of *Anolis* lizards distributed along an altitudinal gradient in the Dominican Republic. They surveyed populations of lizards at sea level, 550 m, 1100 m, and 2200 m altitude. They then compared the percentages of lizards basking and the mean air and lizard body temperatures at the four study sites.




**RESULT:** The percentage of lizards basking increased steadily with altitude. Mean air temperature differed by as much as 8°C among study sites, but mean body temperature differed by only 2°C.

**CONCLUSION:** Lizards living at high altitude bask in patches of sun more frequently, partially compensating for the low environmental temperatures in their habitats.

one full month earlier in the year 2130 than it did in 2000.

A parallel analysis of less detailed data on 677 species of plants and animals suggests that 62% of the species surveyed showed trends toward earlier flowering, breeding, or growth. And for 434 species in which researchers documented a change in geographical distribution, 80% of the shifts were in the direction predicted by climate change models. Parmesan and Yohe noted that geographical distributions change rapidly, and that species respond to both cooling and warming trends. Marine species in Europe expanded their ranges northward during two warming periods in the twentieth century (1930–1945 and 1975–1999), but shifted their ranges southward during a cooling period (1950–1970).

Global warming is also changing species composition and relative abundance within ecological communities. For example, among invertebrates and fishes on the California coast, cold-adapted species have become less abundant and warm-adapted species more abundant. Comparable changes have been noted in communities from Antarctica to the Arctic.

The geographical distributions of species and communities have often changed with climate shifts over evolutionary time, but the rate of global warming has accelerated in your lifetime. As you know from preceding chapters, the factors that govern the structures of communities and ecosystems are complex, and scientists are far from being able to predict all of the consequences of these changes in detail. In the next section, we describe how today's climate affects species and community distributions on a biosphere-wide scale. You can be certain that biology texts in the twenty-second century will paint a very different portrait of these large-scale associations.

### Study Break

1. How does the behavior of *Anolis* lizards in the Dominican Republic change over altitude?
2. What effect is global warming likely to have on the geographical distributions of organisms?

## 52.3 Terrestrial Biomes

In Section 22.2 we described how convergent evolution produces morphological and physiological similarities in species that occupy similar environments. Early

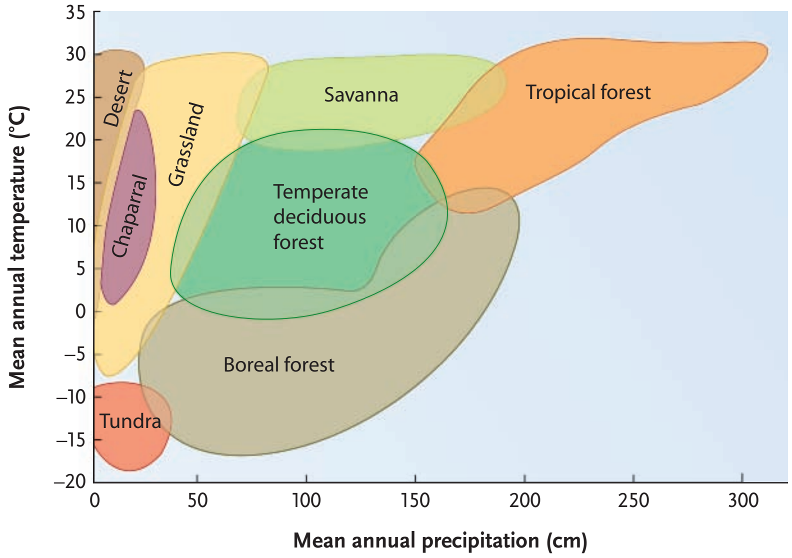



**Figure 52.10**
**Climograph.** Each of the major terrestrial biomes occupies a characteristic combination of temperature and moisture conditions.

in the twentieth century, two American ecologists, Frederic Clements of the Carnegie Institution in Washington and Victor Shelford of the University of Illinois, generalized this observation within a larger perspective by defining the **biome** as a vegetation type plus its associated microorganisms, fungi, and animals. Although vegetation is superficially similar throughout a biome, its species composition varies from place to place. For example, in eastern North America, the temperate deciduous forest biome includes beech-maple forests in the north and oak-hickory forests in the south. Before surveying eight major terrestrial biomes—*tropical forests, savannas, deserts, chaparral, temperate grasslands, temperate deciduous forests, evergreen coniferous forests,* and *tundra*—we consider how environmental factors influence their overall distribution.

## Environmental Variation Governs the Distribution of Terrestrial Biomes

Because organisms—and the communities they form—are sensitive to abiotic factors, climate is the main determinant of biome distribution. A **climograph** portrays the particular combination of temperature and rainfall conditions where each terrestrial biome occurs **(Figure 52.10).** For example, some deserts, grasslands, savannas, and tropical forests occur in areas that have comparable mean annual temperatures but vastly different rainfall. Conversely, some biomes, such as boreal forests, temperate deciduous forests, and savannas, are found under similar moisture conditions but different temperature regimes.

Although the climograph provides a general portrait of the temperature and moisture conditions where the different biomes occur, it does not address the de-

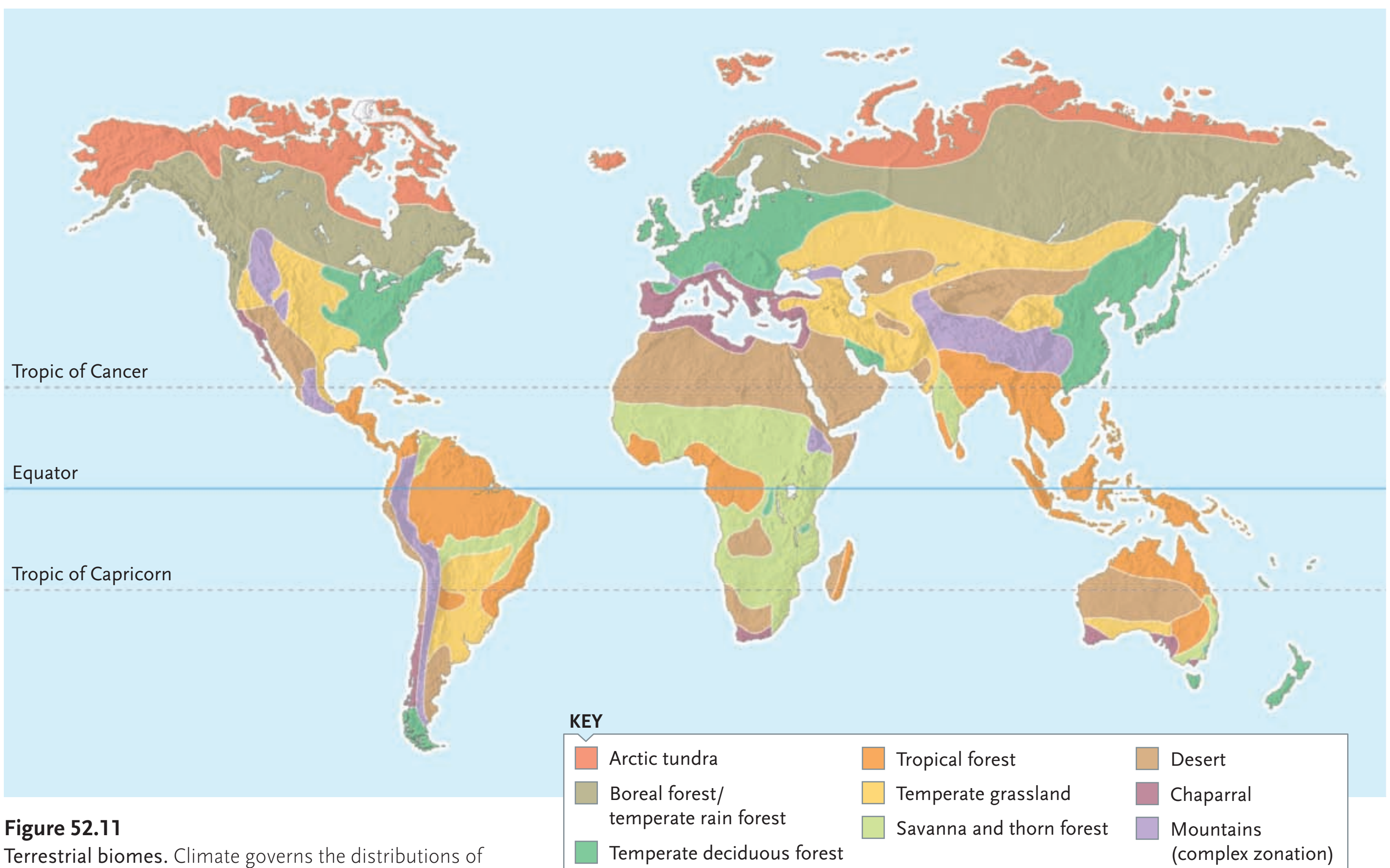



**Figure 52.11**
**Terrestrial biomes.** Climate governs the distributions of the world's major terrestrial biomes.

tails of environmental variation. For example, the climograph includes only mean annual temperature and rainfall, not seasonal variation in these factors. Two regions may have the same mean temperature even though one experiences blazingly hot summers and bitterly cold winters and the other has moderate temperature throughout the year; we would expect them to harbor different organisms. Moreover, the distributions of communities are also influenced by nonclimatic factors, such as regional variations in soil structure and mineral composition (see Section 33.2).

Because temperature and rainfall exhibit latitudinal patterns (displayed in Figures 52.2 and 52.5), the distributions of some terrestrial biomes appear as bands on a world map **(Figure 52.11).** But regional and local climatic variations influence these broad patterns. For example, chaparral is common in certain coastal habitats, whereas grasslands occur further inland at similar latitudes. Comparable bands of distinct vegetation form on mountainsides because temperature and moisture conditions also change with altitude.

## Tropical Forests Include the Most Species-Rich Communities on Earth

Three types of **tropical forests**—rain forest, deciduous forest, and montane forest—sweep across the parts of Africa, Asia, Australia, and Central and South America that receive intense solar radiation and heavy rainfall.

**Tropical rain forests** grow where some rain falls every month, mean annual rainfall exceeds 250 cm, mean annual temperature is at least 25°C, and humidity is above 80%. Limited by neither temperature nor water, the productivity of a tropical rain forest is exceptionally high (see Section 51.1). Trees replace their leaves throughout the year, producing a continuous rain of detritus that ants, land crabs, and other detritivores quickly consume. Decomposers are also active in the hot, moist environment, and almost no litter accumulates on the ground. Because nutrients released by decomposition are promptly absorbed by vegetation or leached by rain, soil in tropical rain forests is nutrient-poor, with low humus content (see Section 33.2).

Tropical rain forests are usually layered (see Figure 50.19). The crowns of tall trees form a dense, tangled canopy that intercepts most incoming sunlight 40 to 45 m above the ground **(Figure 52.12).** Even the largest trees grow only shallow roots in the thin soil, but many have wide *buttresses,* woody lateral extensions of their trunks, that stabilize them in the ground. Shade-tolerant shrubs and small trees form understory layers below the canopy. The woody stems of lianas climb through both layers, and epiphytes, such as bromeliads and orchids, cover the trunks and branches of trees, especially in sunlit openings. In mature rain forests, the ground is surprisingly bare of leafy vegetation, because very little sunlight reaches the forest floor.


**Figure 52.12**
Tropical forest.
Many tropical rain forest trees are covered with lianas and epiphytes.

Tropical rain forests probably harbor more plant and animal species than all other terrestrial biomes combined. Ecologists have proposed numerous hypotheses to explain both the evolution and the maintenance of high species richness in these communities (see Section 50.7), but no single hypothesis explains the pattern adequately. In fact, we do not even have a complete species list for any rain forest community, largely because most animals live in the highly productive canopy, which ecologists have only recently begun to study in detail (see *Focus on Research*). The most extensive tracts of tropical rain forest occur in South America, central and western Africa, and Southeast Asia. Unfortunately, they are being cleared at an alarming rate (see Chapter 53); some experts predict that this biome will all but disappear before the middle of the twenty-first century.

Habitats centered at 20° north and south of the equator experience a pronounced summer rainy season and winter dry season. **Tropical deciduous forests** occur where winter drought reduces photosynthesis, and most trees drop their leaves. For example, the monsoon forests of Southeast Asia, which harbor teak and other tropical hardwoods, are as lush as tropical rain forests in the rainy season; but many trees are bare in the dry season.

High altitudes in the tropics support distinctive **tropical montane forests**, or "cloud forests," which are frequently enveloped in mist. The trees, often no more

## Focus on Research

### Basic Research: Exploring the Rain Forest Canopy

Biological diversity in tropical rain forests has fascinated naturalists for centuries. Sadly, most of its organisms live beyond our reach. The forest canopy extends from 9 or 10 m above the ground to heights as great as 45 m, making the canopy inaccessible and largely unexplored. Early ecologists were able to study canopy-dwelling species only when they found a fallen tree or followed loggers into the forest. In the 1930s, a clever botanist trained monkeys to retrieve plants from the canopy, but these efforts provided little data about the ecological interactions that govern life in the treetops.

Many ecologists still study canopy-dwelling organisms from the safety of the ground. Binoculars provide a good view of fairly large vertebrates. And a hike along a ridge top can provide a canopy-level view of trees growing in an adjacent valley or ravine. Some researchers use ropes to hoist nets or traps into the canopy, lowering them periodically to see what they have caught. Others spray a fog of insecticide into the canopy to kill small invertebrates, which then rain down onto plastic sheets spread below the trees. These ground-based techniques have led to the discovery of hundreds—perhaps thousands—of new arthropod species. Ecologists now collect huge samples of arthropods to study the species composition and structure of communities and to monitor changes in these communities over time. But distant observations and mass sampling techniques don't provide detailed data about which insects are feeding on a tree, how often hummingbirds pollinate a flower, or when a tiny lizard hunts its prey.

Today many ecologists routinely risk life and limb to collect detailed ecological data in the rain forest canopy. They climb trees and crawl along stout branches. Many build stable observation decks with walkways, allowing study on either side of the "trail."

What does this newfound access to the rain forest canopy add to our knowledge of organisms that live there? Researchers can measure the physical environment of the canopy and observe the physiological and behavioral adaptations of its plants and animals. For example, researchers are gathering data on the feeding habits and behavior of small animals that never venture to the ground, such as fruit-eating bats and birds. When coupled with information about the movement patterns of these animals, the data provide insight into the dispersal of seeds in the fruits. And an understanding of seed dispersal provides information for studies of the population ecology of rain forest trees.

Canopy ecologists have also discovered fascinating relationships between plants and their animal pollinators. For example, Donald Perry, a freelance biologist, discovered that birds are attracted to the sweet nectar of the vine *Norantea sessilis*. Feeding birds step on the vine's sturdy flowers; their feet become covered with the plant's pollen, which is embedded in a gummy substance. When the birds visit another vine of the same species, they transfer the pollen to that plant's flowers, providing cross-pollination, which appears to be necessary for the vine's reproduction.

Research in the tropical rain forest canopy promises exciting discoveries about ecological relationships in this unique biome, which is the most threatened on Earth (see Chapter 53). Such research is essential for developing a public appreciation of tropical forests and for creating conservation plans to preserve them.

Nalini M. Nadkarni

A platform in the canopy of a tropical rain forest in Costa Rica provides a comfortable perch for Donald Perry to survey the pollinating activity of birds and bees.

than 3 m tall, are densely covered with epiphytes, which thrive in the moisture-laden air. Cloud-forest plants grow slowly because productivity is limited by low temperatures, high humidity (making transpiration difficult), and sunlight-blocking clouds.

### Savannas Grow Where Moderate Rainfall Is Highly Seasonal

Grasslands with few trees, the biome called **savanna**, grow in areas adjacent to tropical deciduous forests **(Figure 52.13)**. Seasonality in tropical and subtropical savannas is determined by the availability of water; although annual rainfall averages 90 to 150 cm, droughts typically last for months. Grasses are successful in semiarid conditions because their shallow roots harvest water efficiently. With the onset of seasonal rains, they grow quickly, reaching a height of 2 to 3 m. During the dry season, grasses die back and frequently burn, but their underground parts remain alive and resprout when water again becomes available. Shrubby trees outcompete grasses in moist, low-lying areas or on rocky ground, but periodic fires and grazing mammals eliminate most trees as seedlings.

The largest savannas stretch across eastern and southern Africa; smaller patches occur in India, Aus-

© Jonathan Scott/Plant Earth Pictures

**Figure 52.13**
Savanna. The African savanna, a warm grassland with scattered stands of shrubby trees, has an enormous concentration of large ungulates (hoofed, herbivorous mammals), such as these wildebeests *(Connochaetes taurinus)*.

tralia, and South America. African savannas are home to large herbivorous mammals, including antelopes, zebras, giraffes, and elephants, some of which fall prey to savanna predators, such as lions, leopards, cheetahs, and wild dogs. Grazing mammals follow the seasonal cycle of grasses, migrating away from dry areas to greener pastures.

**Thorn forests** grow at the arid borders of true savanna, where large mammals are less abundant. Grasses and other plants that store energy in large underground root systems grow among scrubby trees. Thorn forests are also highly seasonal, growing dramatically in the rainy season and dying back during the annual dry season, which may last for 8 to 9 months.

## Deserts Develop in Places Where Little Precipitation Falls

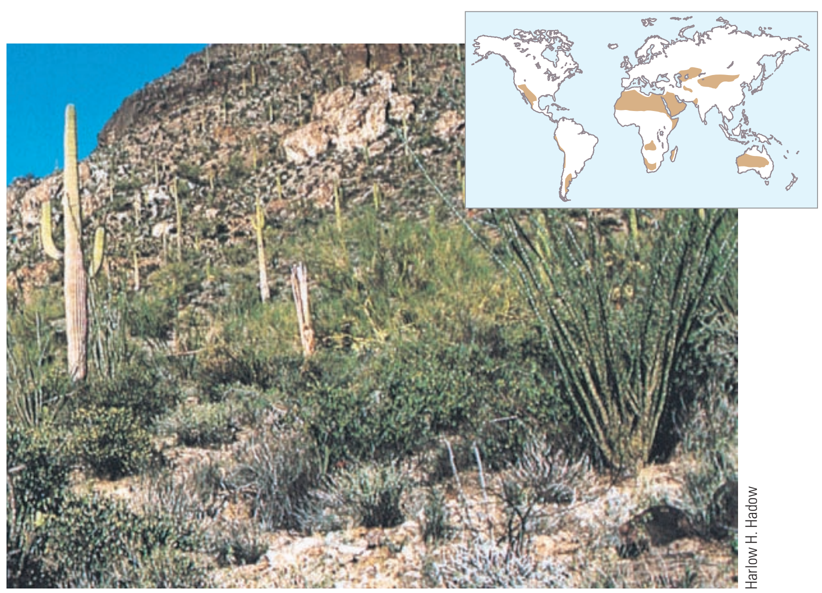
**Deserts** form where rainfall averages less than 25 cm per year. The hot deserts of the American Southwest, northern Chile, Australia, northern and southern Africa, and Arabia occur near 30° latitude, where descending air masses create very dry conditions. Cool deserts, such as the Gobi and Kyzyl-Kum of Asia and the Great Basin of North America, form in massive rain shadows at higher latitudes.

Desert conditions are often extreme. Rainfall arrives infrequently in heavy, brief pulses; and sudden runoff erodes topsoil, which often has high mineral content but little organic matter. Dry air and scant cloud cover allow most sunlight to reach the ground, raising daytime air and ground temperatures as high as 45°C and 70°C, respectively. At night, the surface loses heat quickly; in some deserts, temperatures drop below freezing in winter.

Desert vegetation is always sparse because arid environments do not favor large, leafy plants. Some deserts, such as the Namib of Africa and the Atacama-Sechura of South America, receive so little rainfall that large areas are practically devoid of vegetation. By contrast, the hot Sonoran Desert in northern Mexico, southeastern California, and southern Arizona harbors a diverse flora, including deep-rooted shrubs and shallow-rooted cacti **(Figure 52.14).** Mesquite and cottonwood trees grow deep taproots into the permanent water supply below streambeds. Perennial plants often protect their tissues from herbivores with spines or toxic chemicals, and many use CAM photosynthesis to conserve water (see Section 9.4). After seasonal rains, annual plants germinate, mature, flower, and produce seeds before brutally dry conditions resume.

Deserts also support abundant animals, most of them fairly small. Ants, birds, and rodents often subsist on seeds. Some seed-eating mammals survive on the water they extract from food. Insects, some lizards, and mammals consume the sparse vegetation. Scorpions, lizards, and birds feed primarily on insects; snakes, owls, and foxes prey on other animals. Most

**Figure 52.14**
Desert. The warm Sonoran Desert near Tucson, Arizona, is home to columnar saguaro cacti *(Carnegiea gigantea)* and other drought-adapted plants.



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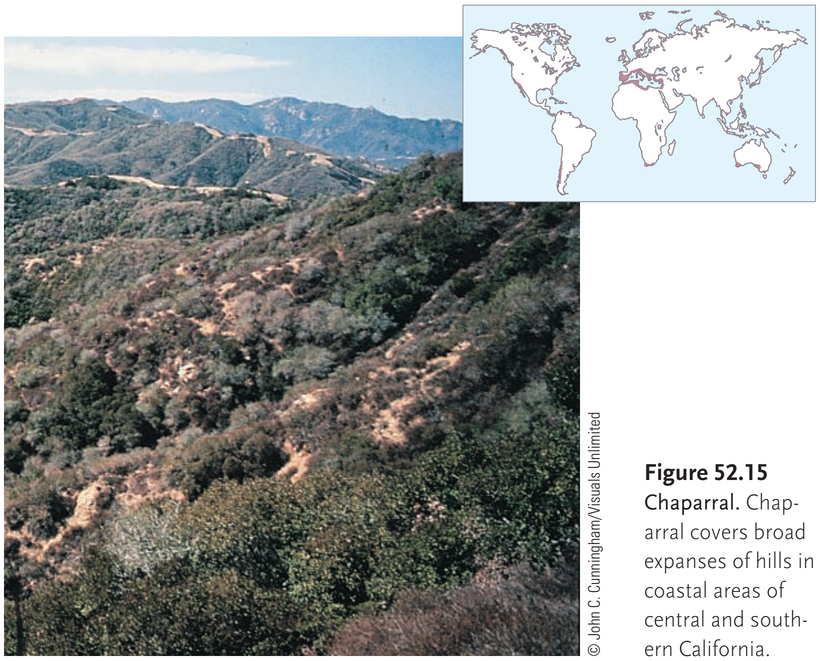

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**Figure 52.15**
**Chaparral.** Chaparral covers broad expanses of hills in coastal areas of central and southern California.

desert animals avoid the midday heat and dehydrating conditions; many retreat into underground burrows, where water vapor from their respiration cools and moistens the air. Many species are nocturnal or active only in the early morning and late afternoon.

## Chaparral Grows Where Winters Are Cool and Wet and Summers Are Hot and Dry

A scrubby mix of short trees and low shrubs called **chaparral** dominates narrow sections of coastal land between 30° and 40° latitude, where winters are cool and wet and summers hot and dry. Seasonal rainfall averages only 25 to 60 cm per year. Chaparral occurs in central and southern California, central Chile, southwestern Australia, southern Africa, and the Mediterranean region.

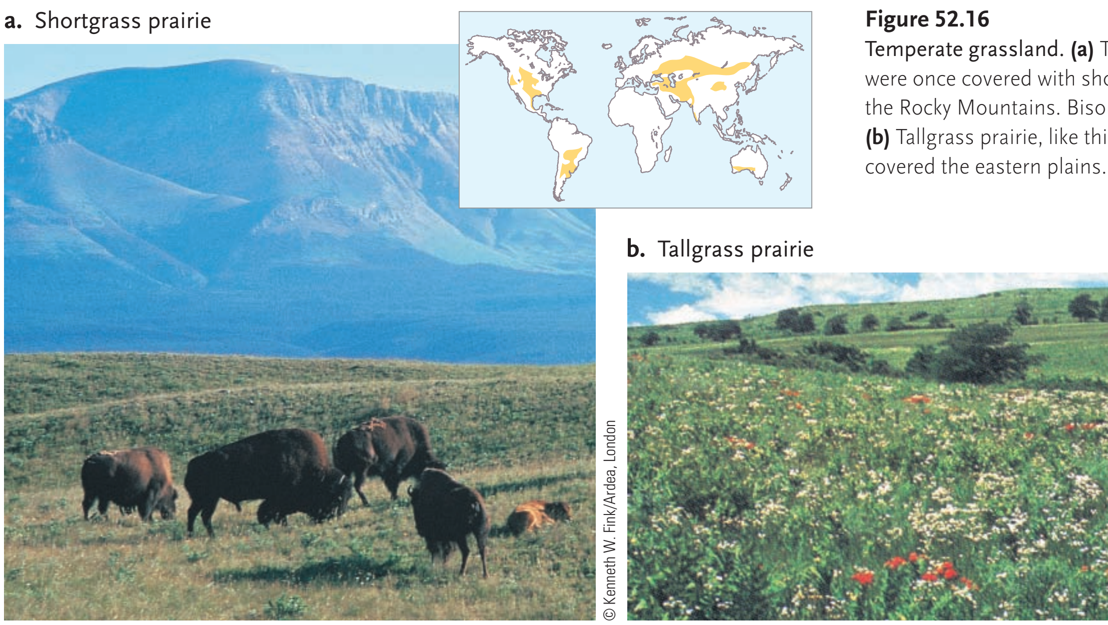
Chaparral shrubs are dense, with hard, tough, evergreen leaves **(Figure 52.15).** They build woody stems above ground and large root systems in the soil. Many species, such as sages (genus *Salvia*), produce toxic, aromatic compounds that inhibit the germination and growth of potential competitors. Just after the winter rains, the shrubs are covered with new leaves and flowers, and the vegetation teems with insects and breeding birds. During the hot, dry summers, however, most plants are dormant, and lightning sparks frequent fires. The aromatic oils and resins of many species, such as eucalyptus, make them highly flammable. Their aboveground parts burn swiftly, but they quickly resprout from large root crowns. Other species release seeds from fire-resistant cones or pods, and their seedlings grow in ash-enriched soil.

## Temperate Grasslands Are Held in a Disclimax State by Periodic Disturbance

**Temperate grasslands** include the prairies of North America, the steppes of central Asia, the pampas of South America, and the veldt of southern Africa **(Figure 52.16).** They stretch across the interiors of continents, where winters are cold and snowy and summers are warm and fairly dry. Only 25 to 100 cm of rain falls unevenly through the year. Temperate grasslands are disclimax communities: seasonal drought, periodic fires, and grazing by mammals inhibit succession, preventing shrubs and trees from displacing perennial grasses and herbaceous plants (see Section 50.6). Grassland soil is rich in organic matter because the aboveground parts of most plants die and decompose annually.

**a.** Shortgrass prairie

**b.** Tallgrass prairie



© Kenneth W. Fink/Ardea, London

© Ray Wagner/Save the Tall Grass Prairie, Inc.

**Figure 52.16**
**Temperate grassland. (a)** The western plains of North America were once covered with shortgrass prairie, as shown here east of the Rocky Mountains. Bison were the dominant large herbivores. **(b)** Tallgrass prairie, like this lush patch in eastern Kansas, once covered the eastern plains.

In North America (see Figure 52.16a) shortgrass prairie covers much of the west, where winds are strong, rainfall light and infrequent, and evaporation rapid. Drought-tolerant perennials have deep roots, and their underground rhizomes, which store energy, resprout quickly after a fire. Tallgrass prairie (see Figure 52.16b) once occupied moister regions to the east of the shortgrass prairie. It boasted an abundance of legumes and sunflowers, often 3 m tall, but most of it was converted to farmland long ago; small patches still exist in nature preserves and in glades within eastern deciduous forests.

North American grasslands are still occupied by large grazing mammals, including pronghorns and bison, which once numbered in the millions. The most familiar burrowing mammal is the prairie dog, a rodent, but pocket gophers, ground squirrels, and jackrabbits are also common. Wolves were the primary large predators until they were hunted nearly to extinction. Coyotes, foxes, ferrets, hawks, and owls still take small prey today.

## Temperate Deciduous Forests Experience Seasonal Dormancy

At temperate latitudes, with warm summers, cold winters, and annual precipitation between 75 and 250 cm, **temperate deciduous forests** grow at low to middle altitudes. In winter, low temperatures reduce photosynthetic rates, and snow and ice can damage leaves. Thus, most plants shed their leaves and grow new ones in spring **(Figure 52.17).** The thick layer of leaf litter, which releases mineral nutrients as it decomposes, enriches the soil. Decomposition is slow, however, because the growing season is only about 7 months long.

Temperate deciduous forests have much lower species richness than tropical forests. Trees form a canopy 10 to 35 m high, and woody shrubs form an understory below it. Herbaceous plants and a ground layer of mosses or liverworts grow below the shrubs. Many herbaceous plants, including some terrestrial orchids, flower early in spring, before trees produce sunlight-blocking leaves; others flower near the end of the growing season.

Forests of ash, beech, birch, chestnut, elm, and oak stretched unbroken across eastern North America, Europe, and eastern Asia before farmers cleared the land. In North America, introduced diseases and insects have nearly eliminated the once dominant species, such as American chestnut and American elm. Today, beech, birch, and maple predominate in the Northeast; oak–hickory forests dominate farther south and west; and oak woodlands merge into tallgrass prairie to the west. Before the arrival of Europeans, deer, bison, bears, and pumas roamed the forests with many smaller species of animals. Today, small mammals such as voles, mice, chipmunks, squirrels, rabbits,

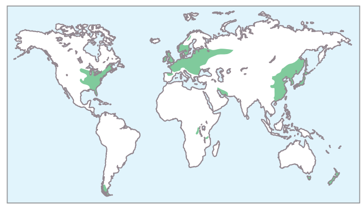



**Figure 52.17**
**Temperate deciduous forest.** Seasonal variations in temperature and water change the character of this forest south of Nashville, Tennessee.

opossums, and raccoons predominate, although deer and bears have recently surged in abundance.

## Evergreen Coniferous Forests Predominate at High Northern Latitudes

The **boreal forest,** or **taiga** (Russian for "swamp forest"), is a circumpolar expanse of evergreen coniferous trees in Europe, Asia, and North America **(Figure 52.18).** Snow blankets the ground during long and extremely cold winters, and most precipitation falls during the short summer. In the northernmost taiga, plants grow quickly during long (18-hour) summer days.

Stands of white spruce and balsam fir dominate North America's boreal forest. Their needle-shaped leaves have a thick cuticle and recessed stomata that conserve water during winter, when ground water is frozen. Fallen needles acidify the thin soil, which speeds the leaching of most nutrients, and few shrubs and herbaceous plants grow beneath the conifers. Lightning-sparked fires are common; some deciduous trees grow in areas opened by fire, but conifers eventually replace them. Cold streams, marshes, ponds, and lakes often dot the landscape; at flat, poorly drained sites, peat mosses, shrubs, and stunted trees dominate acidic bogs, called muskegs.

Most taiga is relatively undisturbed by humans, and it still harbors its native animals. Moose, elk, and deer are the dominant large herbivores. Hare as well as squirrels, porcupines, and other rodents also feed on plants. Some small animals are active all winter in runways they dig beneath the snow. Wolves, lynx, and

Dennis Brokaw

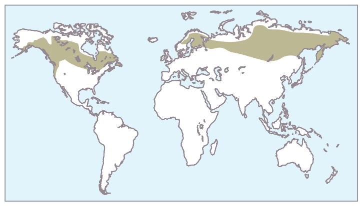


**Figure 52.18**
**Boreal forest.** Single-species stands of spruce dominate this boreal forest, the predominant forest at high latitudes in the Northern Hemisphere.

wolverines prey on herbivores. Grizzly bears and black bears roam the forest, devouring seeds, berries, fishes, and small animals. Mosquitoes, black flies, and gnats are superabundant near bogs and lakes in summer.

Other types of coniferous forest grow in more southerly coastal lowlands where winters are mild and wet and the summers are cool. For example, a **temperate rain forest,** supported by heavy rain and fog, parallels the coast from Alaska into northern California. In western Washington State, the rain forest on the Olympic Peninsula receives 500 cm of rainfall per year, as much as some tropical forests. This temperate rain forest harbors some of the world's tallest trees, including Douglas fir and Sitka spruce to the north and coast redwoods to the south.

## Tundra Comprises a Vast, Treeless Plain in the Northernmost Habitats

The treeless **arctic tundra** stretches from the boreal forests to the polar ice cap in Europe, Asia, and North America. Covering almost 5% of the land, this biome is windswept and wet. Winter temperatures are consistently below freezing. The 2-month summer is so cool that only the topmost layer of soil ever thaws, leaving the ground below perpetually frozen; in some areas, this **permafrost** is more than 500 m thick. Although less than 25 cm of precipitation falls each year, evaporation is slow, and permafrost is impermeable; thus, low-lying soil remains permanently waterlogged, forming bogs **(Figure 52.19a).** Anaerobic conditions and low temperatures retard decomposition, and soggy masses of detritus accumulate.

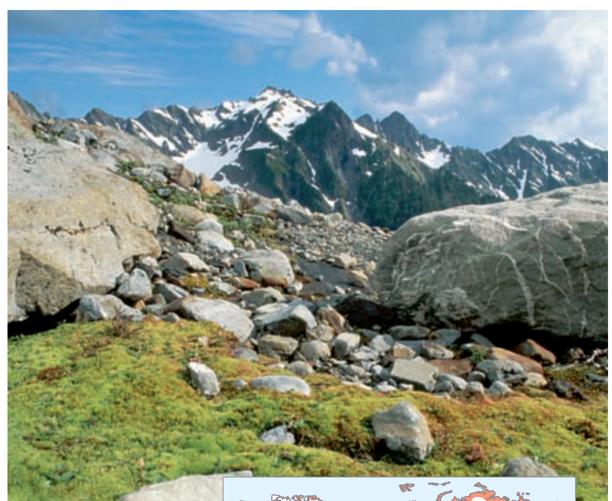
Plants in the tundra are short because the weak sunlight and minimal growing season provide barely enough energy and warmth for net primary productivity; moreover, strong winter winds shred any plants with a high profile. The vegetation consists of low-growing lichens, mosses, grasses, perennial herbs, dwarf shrubs, and a few stunted trees, usually less than 1 m tall. During summer's nearly continuous sunlight, plants flower profusely, and their fruits ripen fast.

Some animals, including herbivorous arctic hares, lemmings, and willow ptarmigans as well as predatory

**a.** Arctic tundra

Dr. Peter Kuhry, Arctic Center, University of Lapland–Finland

**b.** Alpine tundra



© Pat O'Hara/Corbis

**Figure 52.19**
**Tundra. (a)** Rain and snowmelt cannot percolate through the arctic tundra's permafrost. In summer water accumulates in ponds and bogs as shown in this aerial photograph of the tundra in northern Russia. **(b)** Compact, short plants form the alpine tundra, which grows on mountaintops at temperate latitudes, such as the Cascade Range of Washington state.

snowy owls, wolves, foxes, and lynx, are permanent tundra residents. In summer, herds of herbivorous musk oxen, caribou, and reindeer migrate there from boreal forests, and migratory shorebirds and waterfowl arrive to breed. Flying insects abound in summer, especially mosquitoes and black flies, which reproduce in boggy habitats.

A similar biome, called **alpine tundra**, occurs on high mountaintops throughout the world **(Figure 52.19b).** Dominant plants form cushions and mats that withstand the buffeting of strong winds. Winter temperatures are well below freezing, and shaded patches of snow persist even in summer. The thin, fast-draining soil is nutrient-poor, and primary productivity is low.

### Study Break

1. Which terrestrial biomes occur in habitats that receive the greatest amount of rainfall?
2. Which terrestrial biomes are renewed by periodic fires?
3. Which terrestrial biomes have the tallest vegetation? Which ones have the shortest?
4. In which terrestrial biomes are the trees usually evergreen?

## 52.4 Freshwater Biomes

Aquatic biomes comprise several distinctive habitats in either freshwater or marine environments. Freshwater biomes occur where water with a salt concentration below 0.5% accumulates or moves through a landscape. Ecologists distinguish between *lotic* biomes, where water flows through channels, and *lentic* biomes, where water stands in an open basin. All freshwater biomes interact with surrounding land, because runoff carries a nearly constant input of nutrients. Highly productive ecotones, called **wetlands,** often define the borders of freshwater biomes. These marshes and swamps may harbor an astounding array of microorganisms, algae, plants, invertebrates, and vertebrates.

### Streams and Rivers Carry Water Downhill to a Lake or the Sea

The flowing-water biomes start as seeps on high ground. As they flow downhill, they grow into narrow streams, which merge to form wide rivers **(Figure 52.20).** Streams and rivers include three habitats. *Riffles* are shallow, fast-moving, turbulent stretches over a rough bottom of pebbles or rocks. *Pools* are deep, slow-moving areas with a smooth sand or mud bottom. *Runs* are deep, fast-moving stretches over smooth bedrock or sand. Streams generally have high flow rate, low volume, and lots of riffles and pools. As they merge into rivers, flow rate declines, but flow volume increases, and runs and pools predominate. Flow rate and volume also vary seasonally with the rate of water input from rainfall and snowmelt and geographically with altitude and topography.

Physical factors change over the length of a flowing-water system. The concentration of suspended particulate material is low in streams, but high in rivers, which are often turbid with silt. Temperature also increases as water flows downstream to warmer lowland habitats. Because oxygen is more soluble in cold water than in warm water, dissolved oxygen is usually higher in streams than in rivers. Erosion of the streambed and surrounding land provides the solute content of flowing water. Today, agricultural runoff and industrial and municipal wastes provide major input. In unpolluted streams, organic detritus provides more than 95% of the nutrients and energy entering aquatic food webs. This input is particularly important in streams flowing through dense forests, where vegetation blocks the sunlight necessary for primary productivity.

The flow of water affects every aspect of life in streams and rivers. In swift-moving riffles, primary producers cling permanently to fixed substrates, because phytoplankton are swept away by the current. Insect larvae and other invertebrates attach to the un-

**a.** A stream


**b.** A river


**Figure 52.20** Stream and river habitats. **(a)** In streams, such as this one in Virginia, water flows quickly through narrow channels, often with a rocky bottom. **(b)** In rivers, like the Rio Napo in Ecuador, water flows more slowly through broad channels, and suspended sediments often make the water murky.



**Figure 52.21** Lakes. A lake in Torres del Paine National Park, a biosphere reserve in Chile.

dersides of rocks, and many species are flattened, maintaining a low profile in the current. By contrast, large rivers have dense populations of algae and cyanobacteria, which attach to rocks and other substrates, and rooted aquatic plants at the river's edge.

## Lakes Are Bodies of Standing Water That Accumulates in Basins

Lakes and other standing-water biomes are generally fed by rainfall and by streams and rivers that drain surrounding watersheds **(Figure 52.21).** Because the availability of light affects a lake's primary productivity, ecologists often distinguish between the **photic zone** of a lake, the surface water that sunlight penetrates, and the deeper **aphotic zone,** which is always dark.

**Lake Zonation.** Every lake includes zones, defined by depth and distance from the shore, that provide distinctive environments **(Figure 52.22).** In the **littoral zone,** the shallow water near the shore, sunlight penetrates to the bottom. Enriched by nutrients made available by decomposers and runoff, the littoral zone has high productivity and species richness. Rooted aquatic plants, such as cattails and water lilies, grow above the surface, and "floating aquatics," such as duckweed, are common. Submerged vegetation harbors a rich community of microorganisms, epiphytes, and invertebrates. Numerous animals—insects, worms, snails, crayfish, fishes, frogs, turtles, and water birds—use the littoral zone to feed and reproduce.

The **limnetic zone,** the sunlit water beyond the littoral, supports plankton communities: the primary producers are phytoplankton—cyanobacteria, diatoms, and green algae; the primary consumers are zooplankton—rotifers, copepods, and other tiny heterotrophs. Small fishes, which feed on plankton, are themselves consumed by larger fishes, such as bass.

Photosynthesis is impossible, however, in the **profundal zone,** the perpetually dark water below the limnetic zone. Nevertheless, a constant rain of detritus from the limnetic zone supports a community of bacterial decomposers and animal detritivores, including worms, clams, insect larvae, and catfish.

**Seasonal Changes in Temperate Lakes.** In temperate areas, seasonal temperature variations induce changes in the vertical zonation of lakes **(Figure 52.23).** Like other liquids, water gets denser as it cools. But water has a unique property: it reaches maximum density at 4°C, with the density declining as it gets colder. Thus, water at 4°C sinks below water that is either warmer or colder; ice floats because it is less dense than very cold water.

During winter, ice forms on the surface of temperate zone lakes. Water temperature varies from near freezing just below the ice to 4°C at the bottom. Differences in the density of water at 0° and 4°C maintain this thermal stratification. In spring, as the ice melts, the warmer, denser water sinks; and the surface temperature gradually rises to 4°C. For a brief time, the temperature is uniform at all depths. Winds blowing across the lake create vertical currents that cause a **spring overturn,** mixing surface water with deep water. Oxygen at the surface moves to the bottom, and nutrients from the bottom move to the surface.

By midsummer, sunlight heats the top layer of the limnetic zone, called the **epilimnion,** to temperatures above 4°C. In large lakes, the epilimnion may be more than 10 m deep. In the deep water of the lake's profundal zone, called the **hypolimnion,** the temperature remains near 4°C. However, at the boundary between the epilimnion and the hypolimnion, water temperature changes abruptly over a narrow depth range, called the **thermocline.** The thermocline prevents vertical mixing because warm surface water floats above the thermocline, and cool deep water stays below it. During summer, nutrient-rich detritus sinks to the bottom of the lake, where decomposition depletes the oxygen dissolved in the hypolimnion. In autumn, declining sunlight and winds cause the epilimnion to cool, and as the water becomes denser, it sinks, eliminating the thermocline. Winds then mix the water vertically once again during an **autumn overturn,** and dissolved gases and nutrients are equalized at all depths.

Primary productivity in the limnetic zone varies with the seasonal overturns. In spring, increased sunlight, warm temperatures, and the sudden

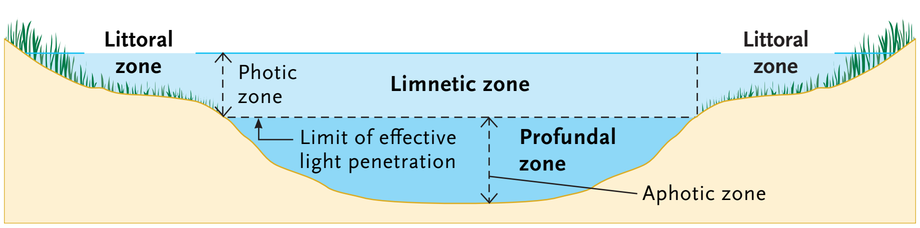



**Figure 52.22** Lake zonation. The zonation in a lake is based upon the water's depth and its distance from shore.

availability of nutrients induce a bloom of productivity. As the season progresses and the thermocline prevents vertical mixing, nutrient levels dwindle in the epilimnion, and primary productivity declines. By late summer, nutrient shortages limit photosynthesis. After the autumn overturn, nutrient cycling drives a short burst of primary productivity. But as days get shorter and temperature declines, primary productivity remains low until spring.

**Trophic Nature of Lakes.** Ecologists classify lakes by their nutrient content and rates of productivity. **Oligotrophic lakes** are poor in nutrients and organic matter, but rich in oxygen. Their low primary productivity keeps the water crystal clear, making them popular recreational sites. By contrast, **eutrophic lakes** are rich in nutrients and organic matter. The decomposition of organic matter depletes oxygen in the hypolimnion when the lake is stratified, and high primary productivity in the epilimnion often chokes the water with seasonal blooms of cyanobacteria and filamentous algae. Eutrophic lakes are often thick and "soupy," making them unattractive for recreation. Over long periods of time, as sediments accumulate, lakes naturally change from oligotrophic to eutrophic; their basins eventually fill with sediments, and terrestrial plants invade.

As you learned in the description of changes in Lake Erie at the beginning of Chapter 51, the addition of nutrients to a lake often disrupts its trophic condition. In a classic experiment conducted in the late 1960s, David Schindler and his colleagues at The Experimental Lakes Project in Ontario, Canada, experimentally separated the two basins of a lake with a plastic curtain. The researchers added phosphates to one basin and used the other basin as a control. Within 2 months, the artificially enriched basin sported a bloom of cyanobacteria, a sign of eutrophication; the control basin remained oligotrophic and crystal clear **(Figure 52.24).**

### Study Break

1. How does the availability of dissolved oxygen vary from the headwaters of a stream to the mouth of a river?
2. What factors cause the seasonal overturns in lakes?
3. Why are oligotrophic lakes better for recreational purposes than eutrophic lakes?

## 52.5 Marine Biomes

Marine biomes, in which salinity (salt concentration) averages about 3%, cover nearly three-fourths of Earth's surface and account for a large fraction of its primary productivity. They also mediate important global processes: marine phytoplankton process large amounts of carbon dioxide, generating oxygen and moderating the greenhouse effect.

As with standing freshwater biomes, depth and distance from shore govern the physical characteristics of marine habitats. Ecologists describe ocean zonation in several ways **(Figure 52.25),** including the distinction between the photic and aphotic zones. Another major distinction is between the **pelagic province,** the water, and the **benthic province,** the bottom sediments. The pelagic province includes the **neritic zone,** the shallow water above the continental shelves, and the **oceanic zone,** the deep water beyond them. The benthic province is divided into the **intertidal zone,** the shoreline that is alternately submerged and exposed by tides, and the **abyssal zone,** the bottom sediments that lie permanently below deeper water. Here we describe five marine biomes—*estuaries, rocky and sandy coasts, continental shelves and oceanic banks, open ocean,* and *benthic regions*—that represent particular associations of organisms occupying different marine zones and provinces.

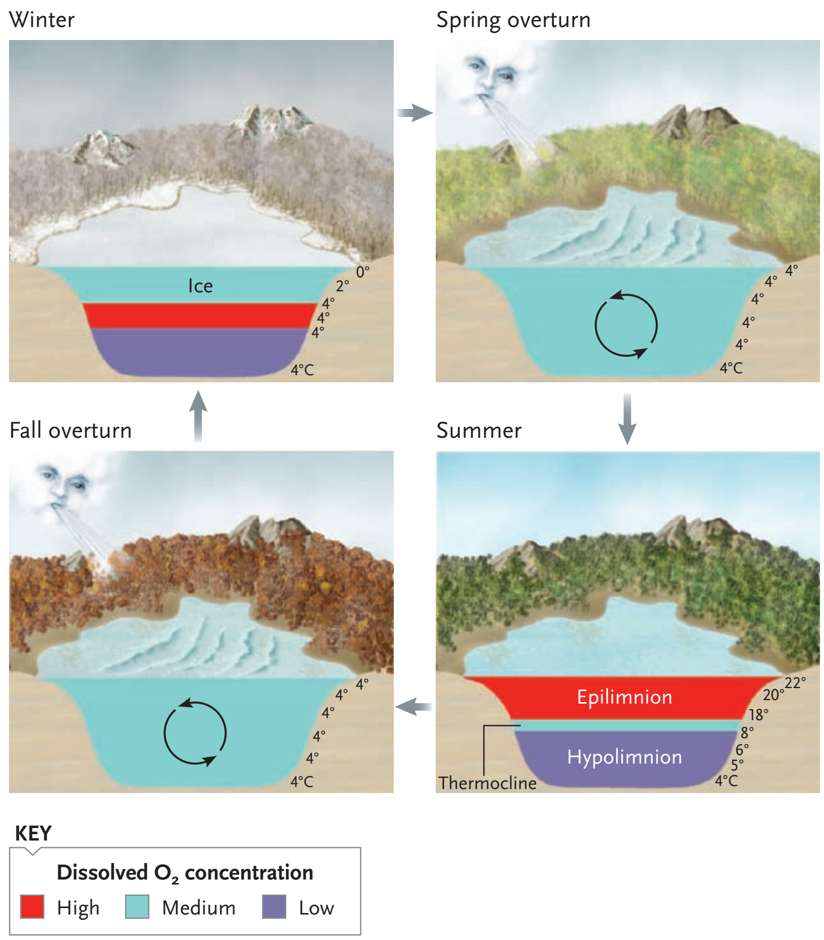



**Figure 52.23**
Seasonal overturns in lakes. The waters of shallow temperate-zone lakes mix twice each year. During the spring and autumn overturns, temperature is equalized at all depths; nutrients are carried upward from the bottom; and oxygen is carried downward from the surface.

## Figure 52.24 Experimental Research

### *Artificial Eutrophication of a Lake*

**QUESTION:** Does the addition of excess phosphorus to a lake encourage the growth of primary producers, such as cyanobacteria?

**EXPERIMENT:** Schindler and his colleagues experimentally separated the two basins of a lake in Ontario, Canada, with a plastic curtain. The researchers added phosphates to one basin and used the other basin as a control.

**RESULTS:** Within 2 months, the artificially enriched basin (in the upper left of the photo) sported a pale green bloom of cyanobacteria, a sure sign of eutrophication; the control basin remained oligotrophic and crystal clear.

D. W. Schindler, *Science*, 897–899

**CONCLUSION:** The addition of excess phosphorus to a lake encourages blooms of cyanobacteria, causing the lake to change from oligotrophic to eutrophic.

### Estuaries Form Where Rivers Meet the Sea

**Estuaries** are coastal regions where seawater mixes with fresh water from rivers, streams, and runoff **(Figure 52.26).** Salinity is low where fresh water enters the estuary and high on the tidal side. After heavy rainfall, fresh water floods into the habitat, reducing salinity and raising water temperature. At high tide, cold, salty water flows in from the sea. All estuarine organisms must tolerate these variable conditions.

Variations in local topography influence an estuary's physical features. Chesapeake Bay in Maryland, Mobile Bay in Alabama, and San Francisco Bay in California are broad, shallow estuaries. The estuaries in Alaska and British Columbia are narrow and deep, as are Norway's fjords. Many estuaries are bordered by **salt marshes,** tidal wetlands dominated by emergent grasses and reeds (see Figure 52.26a). In tropical estuaries, the roots of densely packed mangrove trees penetrate the muddy bottom, accumulating sediments and slowly adding land to the shoreline (see Figure 52.26b).

The constant input of nutrients and removal of wastes by the tides contribute to exceptionally high productivity in estuaries. Primary producers include phytoplankton, salt-tolerant grasses and reeds that can withstand submergence at high tide, and algae that grow in mud and on plant surfaces. Roots and stems trap organic matter, which enters detrital food webs. The detritus (and bacteria clinging to it) supports nematodes, snails, crabs, and fishes; suspension-feeding mollusks and arthropods capture edible particles in the slowly moving water. Many marine arthropods and fishes breed in calm, shallow estuaries, where their young find abundant food and refuge from predators in the complex vegetation. Migratory birds use estuaries as rest stops, and shore birds and waterfowl use their muddy bottoms as rich feeding grounds, particularly at low tide.

### Rocky and Sandy Coasts Experience Cyclic Periods of Exposure and Submergence

The intertidal zone, the area between low and high tide marks, is one of the most stressful habitats on Earth. On rocky shores, residents are battered by waves and floating debris. Sessile species, such as mussels and barnacles, attach to substrates with special structures or cement. Motile species, such as limpets and sea stars, simply hang onto rocks. Organisms that live high on the shore dry out at low tide, freeze in winter, and bake in summer. Exposed animals often seal themselves inside shells, and intertidal algae have thick polysaccharide coats that adsorb water and prevent dehydration.

Biotic interactions also take their toll. Organisms throughout the intertidal zone compete for attachment sites to avoid being washed away (see Figure 50.12). At low tide, predatory birds and mammals attack from above; at high tide, predatory fishes move in from the sea. Because the tides often scour detritus from the rocky intertidal, grazing food webs predominate.

Rocky shores often have three zones **(Figure 52.27).** The *upper intertidal* is submerged only during the highest tide of the lunar cycle. It is sparsely populated by barnacles, sturdy algae, and grazing and predatory snails. The *middle intertidal* is submerged daily during the highest regular tide and exposed during the lowest. Its tide pools are occupied by red, brown, and green algae, grazing and predatory mollusks, sponges, sea anemones, worms from several phyla, hermit crabs, echinoderms, and small fishes. Biodiversity is greatest in the *lower intertidal,* which is exposed only during the lowest tide of the lunar cycle. It is occupied by dense beds of algae, tunicates, echinoderms, other invertebrates, and fishes.

Sandy shores are composed of loose sediments that waves and currents constantly rearrange. Large plants cannot grow on such unstable substrates, so grazing food webs are rare. Organic debris imported from offshore or from nearby land supports detrital food webs. Animals live in burrows, which they must frequently repair as the substrate shifts. Crabs and shorebirds live as scavengers or predators above the high tide mark. At night, beach hoppers and ghost crabs leave their burrows, seeking food. Marine worms, clams, crabs, and other invertebrates live in the sand between the high and low tide marks.

## Light Penetrates the Shallow Water over Continental Shelves and Oceanic Banks

The neritic zone includes the shallow water over continental shelves and oceanic banks, underwater landmasses that rise to within 300 m of the surface. Although small in area, the neritic zone is highly productive and species-rich **(Figure 52.28).** Runoff from the land brings a steady inflow of nutrients; and upwelling and waves circulate nutrients from the bottom to the photic zone.

In temperate regions, giant kelp forests, which are among Earth's most productive ecosystems, occupy some continental shelves and banks (see Figure 52.28a). Kelp are enormous algae that attach to the bottom with giant holdfasts; their stipes ("stems") reach upward with fronds fanning out into the water. Sea anemones, snails, echinoderms, lobsters, and other invertebrates live in the kelp, where fishes and other predators consume them. Even where kelp does not grow, continental shelves and banks teem with life. Most of the important fisheries in the temperate zone occur there.

In the tropics, the warm but nutrient-poor water above continental shelves is often occupied by **coral reefs** (see Figure 52.28b). Sunlight penetrates the clear water all the way to the bottom. Photosynthetic dinoflagellates, living as endosymbionts of the coral animals (see Section 26.2), and coralline algae are largely responsible for primary productivity. Coral animals also feed on microscopic organisms and suspended particles. The reefs are the remains of corals, algae, and other organisms, and their structural complexity rivals that of tropical rain forests. Tides and currents carve ledges and caverns; and storms frequently disturb the reefs, creating openings in which new coral colonies can grow (see Section 50.5). A reef may be festooned with as many as 750 species of corals and a dizzying variety of algae. The diversity of coral skeletons provides a complex structure that is used by invertebrates from nearly every phylum and by a host of herbivorous and carnivorous fishes.

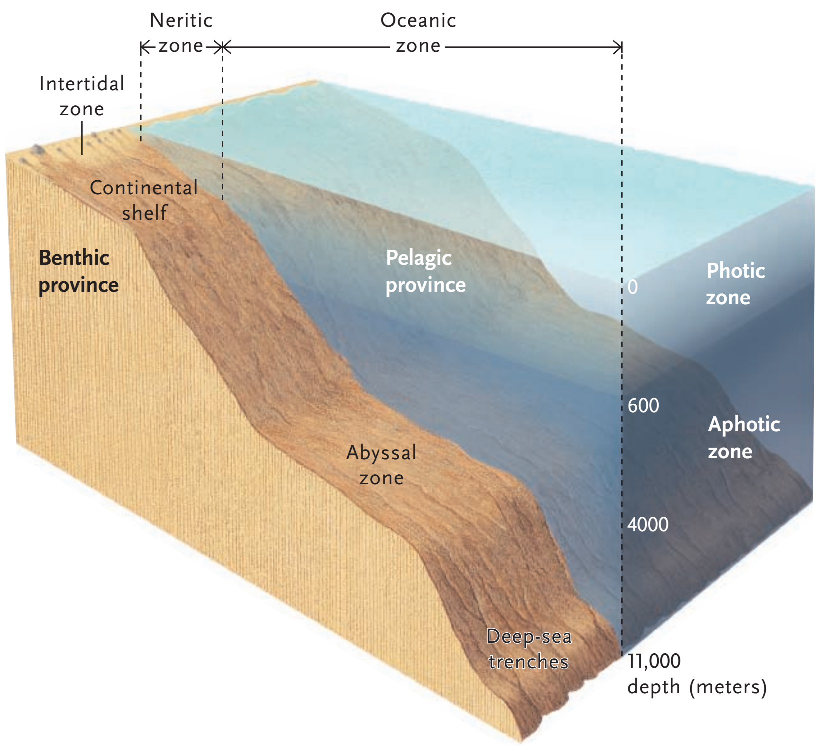



**Figure 52.25**
Oceanic zonation. Ecologists divide the ocean into the pelagic province (the water) and the benthic province (the ocean bottom). Zones are defined according to the depth of water (photic versus aphotic zones) and distance from shore (neritic versus oceanic zones in the pelagic province, intertidal versus abyssal zones in the benthic province). The different zones are not drawn to scale.

**a.** Salt marsh grasses



**b.** Mangroves



**Figure 52.26**
Estuaries. **(a)** The salt marsh grass (*Spartina* species) is the major producer in a South Carolina estuary. **(b)** Red mangroves *(Rhizophora mangle)* are abundant in Florida's Everglades.

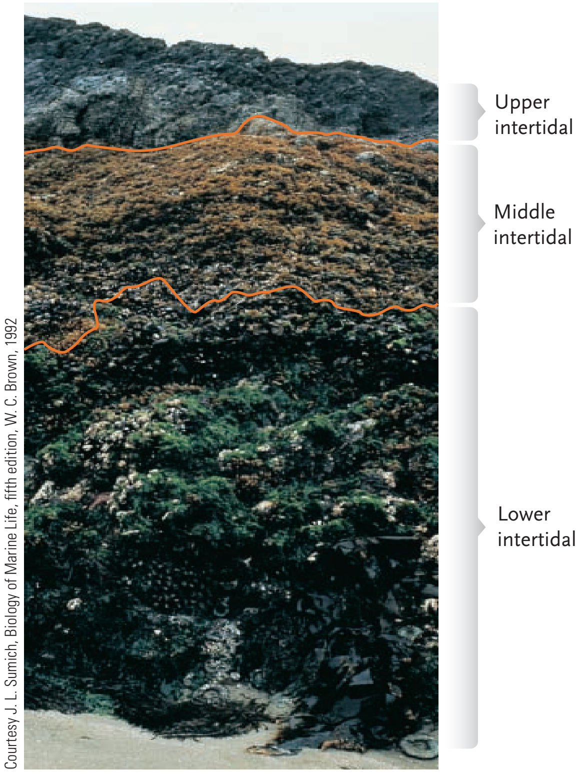



**Figure 52.27**
Vertical zonation in the intertidal. A rocky shore in the Pacific Northwest clearly exhibits the characteristic vertical zonation. The distance between low and high tide marks on this rocky shore is about 3 m.

## In the Open Ocean, Photosynthesis Occurs Only in the Upper Layers

The oceanic zone lies beyond the continental shelves. Though generally low in nutrients, it is locally enriched by runoff from land and by upwelling bottom waters. The open ocean is typically cold, except in the tropics. The surface water is illuminated by sunlight, which warms it somewhat and allows photosynthesis. Most primary productivity is restricted to a depth of about 50 m, however, because seawater filters light. Photosynthetic activity varies seasonally, as it does on land.

"Pastures" of phytoplankton are eaten by zooplankton, including copepods, shrimplike krill, small worms, cnidarians, and the larvae of invertebrates and fishes. Consumers that can actively swim against the currents, such as squids, fishes, marine turtles, and whales, are called **nekton (Figure 52.29).** Some consumers feed on plankton, and some prey on other nekton. Low light levels in water between about 50 and 600 m allow little photosynthesis, but many fishes and some mobile invertebrates are active at these depths, traveling into the sunlit zone to feed on organisms near the surface.

No sunlight ever penetrates the deepest part of the oceanic zone below 600 m. Some of these abyssal regions, such as the Marianas Trench, are more than 9 km below the surface. Scientists have explored the deepest water in the ocean only during the past few decades, but we know that it is a cold (2° to 3°C), dark environment, where organisms live under tremendous pressure from the ocean above. Abyssal communities are surprisingly diverse, although population densities tend to be low. The denizens of the abyssal zone include invertebrates, bony fishes, and sharks. Some fishes and invertebrates are bioluminescent, producing spots of light that may serve for communication or as lures to entice prey within reach of their large jaws **(Figure 52.30).**

## The Benthic Province Includes the Rocks and Sediments of the Ocean Bottom

The benthic province extends from the intertidal zone to the deep-sea trenches. In the oceanic zone, bottom sediments are composed of soft mud, fine particles of silt, detritus, and the shells of dead microscopic organ-

**a.** Kelp forest **b.** Coral reef

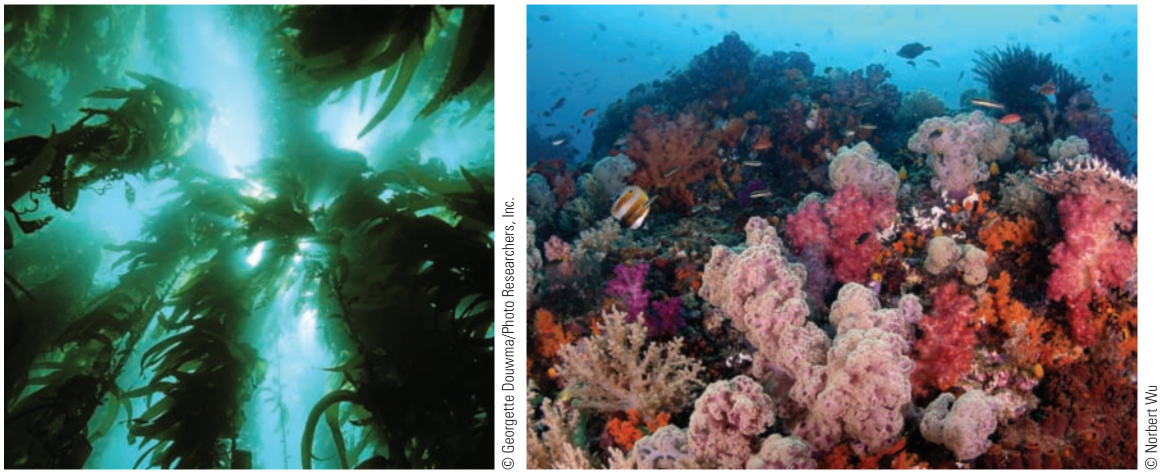



**Figure 52.28**
Neritic zone. **(a)** Kelp forests, such as this one off the coast of California, often grow in the neritic zone along the coast at temperate latitudes. **(b)** This coral reef in the Raja Ampat islands of Indonesia illustrates the structural complexity and biological diversity found in reef communities.

isms. Species living in and on the bottom are collectively called **benthos.** Sunlight never strikes the benthic province of the open ocean, which is inhabited by bacteria, fungi, and a variety of animals. Sessile invertebrates, such as sponges, sea anemones, and clams, live amidst the sediments, and many motile animals, including worms, mollusks, crustaceans, echinoderms, and fishes, form detrital food webs supported by organic remains that sink from pelagic communities.

In 1976, researchers found communities thriving near hydrothermal vents at a depth of 3000 m near the Galápagos Rift, a volcanically active boundary between two crustal plates. Near-freezing water seeps into fissures where it is heated to temperatures of 350°C or higher. Pressure forces the heated water upward, and minerals are leached from porous rocks as the water spews out through vents in the seafloor. This hydrothermal outpouring releases hydrogen sulfide, which serves as an energy source for chemoautotrophic bacteria, the primary producers in hydrothermal vent communities. Some of these bacteria live as endosymbionts of giant clams and tube-dwelling worms **(Figure 52.31).** Deep-sea food webs also include sea anemones, crustaceans, and fishes. Researchers have located hydrothermal vent ecosystems in the South Pacific, near Easter Island; in the North Pacific, off the coast of British Columbia; the Gulf of California, about 150 miles south of the tip of Baja California, Mexico; and the Atlantic.

Recent research in the deepest reaches of the ocean reveals that communities also exist in areas far from hydrothermal vents. These "cold seep" communities thrive on broad expanses of the seafloor, where extremely salty water percolates upward from the underlying rocks and sediment, carrying abundant minerals, hydrogen sulfide, and methane to areas that are accessible to organisms. Chemosynthetic bacteria, which grow in large mats, can metabolize these molecules, forming the base of food webs that also include sponges, worms, and bivalve mollusks.

## Study Break

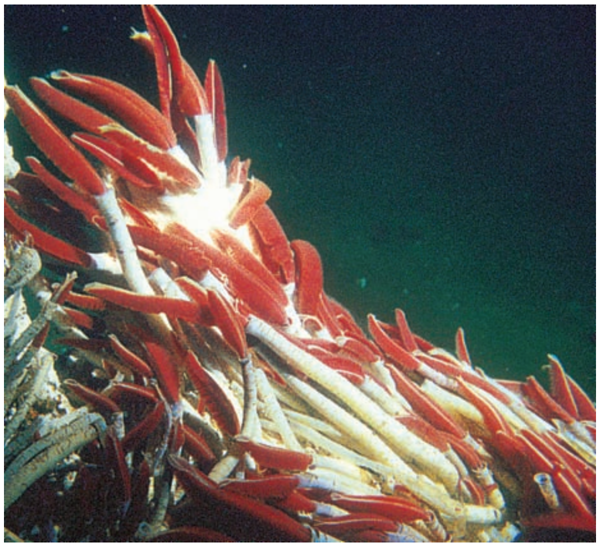
1. What is the difference between the benthic and pelagic provinces of the ocean?
2. Which marine biomes experience the largest fluctuations in salinity (salt concentration) over time?
3. Which marine biomes or regions within marine biomes receive abundant energy input from sunlight?
4. What is the source of nutrients and energy for the benthos of the oceanic zone?
5. What organisms are the primary producers in hydrothermal vent and cold seep communities, and how do they differ from the primary producers in the photic zone?

McCutcheon/ZEFA

**Figure 52.29**
**Open ocean.** A humpback whale *(Megaptera novaeangliae)* breaches (leaps out of the water) near a British Columbia coastline.

David Shale/npl/Minden Pictures

**Figure 52.30**
**Deep sea.** A deep-sea anglerfish (*Himantolophus* species) uses a bioluminescent lure to attract prey to its formidable jaws.



Robert Vrijenhoek/MBARI

**Figure 52.31**
**Deep benthos.** Giant tube-dwelling worms are common in the hydrothermal vent communities on the deep ocean floor.

## Unanswered Questions

**How will biomes change in response to anthropogenic (human-induced) global warming?**

Will biomes remain largely intact and simply shift their geographical distributions northward or upward (to higher altitudes)? Or will the biomes we recognize today become disrupted, and new biomes arise as species associate in different combinations? Parmesan and Yohe estimated that 59% of wild species around the world have already shown some change in their geographical distributions in response to the relatively small level of global warming—a 0.7°C rise in average temperature—over the past 100 years. Documented responses to global warming vary from species to species, however. For example, only 20% of butterfly species in Spain, France, and North Africa have shifted their southern range boundaries northward, but 70% of butterfly species in the United Kingdom and Scandinavia have expanded their northern range borders further northward, sometimes by as much as 300 km over the past 30 years.

Thus, although the distributions of some species appear stable, the ranges of others are showing strong responses to global warming. At least two hypotheses may explain these patterns. First, some species may be stressed by rising temperatures but have not yet shown a measurable response. Second, the geographical distributions of some species may not be governed primarily by climate. Whatever the reason, the fact that we observe large variation in the response of different species suggests that not all species in a community are moving together. Thus, the existing communities of birds, butterflies, and trees are being disrupted—with some species moving and others not. Biologists have also noted differences in the response of different taxonomic groups. Butterflies in Europe and North America seem to be shifting their distributions northward and upward at about the same rate that temperatures are changing, but plants appear to lag behind. Alpine herbs in Switzerland, for example, have shifted their distributions upward at about half the rate that one might expect from the rate of regional warming, and it was 30 years after warming began before tree seedlings in Sweden started to colonize alpine habitats at higher elevations, shifting the treeline upward.

Even bigger questions remain. Will the vegetation that currently lives in the tropics expand into what is now the temperate zone and cover more of the planet? Some studies suggest that tropical lowland trees are already at their physiological limit—already showing signs of stress by shutting down photosynthesis on the hottest and driest days. Furthermore, climate model projections from a 2007 report of the Intergovernmental Panel on Climate Change consistently show substantial drying as well as warming in midlatitudes. If this projection is correct, many plants and animals now living in the wet tropics will be unable to shift northward into what may become an extreme desert climate. And what will happen to the arctic tundra? Researchers have already collected strong evidence that shrubs and trees are encroaching northward into the tundra of Alaska and Canada. The permafrost is melting, and the soil is drying. How do these observed changes in plant and animal distributions relate to the future? Human activity has already caused Earth's mean annual temperature to rise by 0.7°C in the past 100 years. Climate model projections suggest that further increases between 1.8°C and 4.0°C are likely; some models suggest the rise will be over 6.0°C. Can the tundra biome survive even the lowest projections—more than twice the warming it has already experienced?

**How will evolution shape the ways that wild species respond to climate change? Which groups of organisms are likely to adapt, and which are likely to become extinct?**

Populations are evolving all the time in response to changing selection regimes. Global warming is one of many human-driven environmental changes that could foster genetic change. Biologists have known for decades that organisms are locally adapted to the climatic conditions under which they routinely live. Scientists have documented local genetic changes toward more warm-adapted genotypes in fruit flies, mosquitoes, and the algal symbionts of corals. Do the observed genetic changes suggest that these species are adapting to anthropogenic global warming? Will other species follow suit? The fossil record suggests that during the Pleistocene glaciations, when Earth's temperature shifted between glacial periods (4°–8°C colder than now) and interglacial periods (today's temperatures), very few species became extinct and few experienced substantial morphological evolution. But, before the Pleistocene, Earth was much hotter than it is today, and the atmosphere had higher levels of $CO_2$. During the transition from these very warm, high $CO_2$ conditions to the colder, low $CO_2$ conditions of the Pleistocene, a large proportion of species became extinct. To how much climate change can organisms adapt? At what point is climate change extreme enough that species come to the limit of their genetic variation, can no longer adapt, and become extinct?

Camille Parmesan is an associate professor in the Section of Integrative Biology at the University of Texas at Austin. Her recent work has focused on current impacts of climate change on wildlife, and especially on butterfly range shifts. To learn more about her research, go to http://cluster3.biosci.utexas.edu/research/parmesanLab.

## Review

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### 52.1 Environmental Diversity of the Biosphere

- The biosphere encompasses all the regions on Earth where organisms live, including the atmosphere, hydrosphere, and lithosphere.
- Latitudinal variations in solar radiation establish global climate patterns (Figure 52.2). Earth's tilt on its axis causes seasonal variation in solar radiation and climate (Figure 52.3). Seasonal variations in day length and temperature increase steadily from tropical latitudes toward the poles.
- Unequal heating of the atmosphere causes air masses to flow in circulation cells that create worldwide wind and precipitation patterns (Figures 52.4 and 52.5). Ocean currents generally flow clockwise in the Northern Hemisphere and counterclockwise in the Southern Hemisphere (Figure 52.6).
- The oceans and local topographical features influence regional and local climates. Proximity to the ocean has a moderating effect on terrestrial climates (Figure 52.7). Habitats are generally wetter on the windward sides of mountains than on the leeward sides (Figure 52.8).

Animation: Global air circulation patterns

Animation: Air circulation and climate

Animation: Major climate zones and ocean currents

Animation: Rain shadow effect

Animation: El Niño Southern Oscillation

### 52.2 Organismal Responses to Environmental Variation

- Organisms use homeostatic responses to cope with environmental variation. Animals often use facultative behavioral and physiological mechanisms to respond to environmental temperature (Figure 52.9).
- Global warming is affecting the ecology of many organisms. Many species are experiencing changes in their geographical ranges or in the timing of their reproduction.

### 52.3 Terrestrial Biomes

- Biomes are general types of vegetation and other associated organisms. Climate is the major determinant of terrestrial biome distributions (Figures 52.10 and 52.11).
- Tropical forest occurs at low latitudes where seasonality is determined by variations in rainfall rather than by day length and temperature (Figure 52.12). Tropical rain forests are the most species-rich terrestrial biome, but they grow on nutrient-poor soils.
- Savanna is tropical and subtropical grassland with scattered trees (Figure 52.13). Long dry seasons, fires, and grazing by large mammals prevent trees from replacing perennial grasses.
- Deserts form in arid regions where precipitation is low and temperature varies widely on a daily and seasonal basis (Figure 52.14).
- Chaparral is a coastal biome dominated by dense, woody shrubs and trees that resprout after periodic fires (Figure 52.15). Chaparral occurs where winters are mild and wet and summers hot and dry.
- Temperate grassland grows where winters are cold, summers are warm, and rainfall is moderate (Figure 52.16). Tree seedlings are eliminated from grasslands by droughts, periodic fires, and grazing by mammals. Grassland soils are rich and deep.
- Temperate deciduous forest flourishes at middle latitudes with abundant rainfall. The seasonality of the climate is reflected in the annual loss and regrowth of leaves (Figure 52.17).
- The boreal forest, or taiga, includes dense stands of coniferous trees at high latitudes, where winters are long and cold (Figure 52.18).
- Tundra is the northernmost biome, where plants grow in shallow topsoil over a layer of permafrost (Figure 52.19). The brief growing season and winter winds cause tundra plants to be very short.

Animation: Terrestrial biomes

Animation: Soil profiles

### 52.4 Freshwater Biomes

- Freshwater biomes include both flowing-water and standing-water systems.
- The physical characteristics of flowing-water biomes change from the headwaters of a stream to the mouth of a river (Figure 52.20), and their food webs are largely detrital.
- The physical characteristics of standing-water biomes change with the depth of water and distance from shore (Figures 52.21 and 52.22). Lakes exhibit marked vertical zonation and, in the temperate zone, undergo a seasonal mixing of their waters (Figure 52.23). Lakes are generally classified by their nutrient status and productivity (Figure 52.24).

Animation: Lake zonation

Animation: Lake turnover

Animation: Trophic nature of lakes

### 52.5 Marine Biomes

- The world's oceans exhibit marked zonation based on water depth and distance from shore (Figure 52.25).
- Estuaries are highly productive tidal biomes where rivers provide a constant input of nutrients and freshwater, and the tides carry away wastes (Figure 52.26).
- The intertidal zone is a stressful environment that is alternately submerged and exposed (Figure 52.27).
- Highly productive and diverse shallow-water biomes grow on continental shelves and oceanic banks. Kelp forests predominate at high latitudes, whereas coral reefs occur in the tropics (Figure 52.28).
- The open ocean is highly stratified because photosynthesis is possible only in the uppermost 50 m of water. Plankton are the primary producers in the uppermost layers; they support grazing food webs (Figure 52.29). The deep sea includes many predatory species (Figure 52.30).
- Organisms of the sea floor occupy the benthic province. Falling detritus supports most benthic communities, but chemoautotrophic bacteria support communities near deep-sea hydrothermal vents (Figure 52.31).

Animation: Rocky intertidal zones

Animation: Three types of reefs

Animation: Oceanic zones

Animation: Coastal upwelling

Animation: Hydrothermal vent community

# Questions

## Self-Test Questions

1. The lithosphere includes all:
   a. oceans.
   b. ice caps.
   c. rocks, soils, and sediments.
   d. gases and airborne particles.
   e. places where organisms live.
2. Earth's 23.5° tilt on its axis directly causes:
   a. latitudinal variation in average annual rainfall.
   b. ocean currents to rotate clockwise in the Northern Hemisphere.
   c. microclimates to vary dramatically over short distances.
   d. low rainfall on the leeward side of mountain ranges.
   e. seasonal variation in the amount of solar radiation.
3. Adiabatic cooling causes rising air masses to:
   a. absorb moisture from Earth's surface.
   b. release precipitation.
   c. change the direction of the El Niño current.
   d. flow toward the equator from the poles.
   e. be deflected from a strictly northward or southward flow.
4. The term "rain shadow" describes the:
   a. low rainfall that is typical on the leeward side of mountains.
   b. low rainfall that is typical at 30° latitude.
   c. high rainfall that is typical on the windward side of mountains.
   d. blocking of rain by vegetation in dense tropical forests.
   e. low rainfall that is typical in the interior of continents.
5. The major climatic factors that govern the distributions of terrestrial biomes are:
   a. temperature only.
   b. rainfall only.
   c. wind speed only.
   d. temperature and rainfall.
   e. temperature, rainfall, and wind speed.
6. Which biome experiences the highest annual rainfall?
   a. tropical rain forest
   b. tropical savanna
   c. chaparral
   d. temperature grassland
   e. arctic tundra
7. From which biome are trees excluded by periodic fires and grazing herbivores?
   a. tropical rain forest
   b. thorn forest
   c. chaparral
   d. temperate grassland
   e. arctic tundra
8. The major source of nutrients in the headwaters of a small stream is from:
   a. dead leaves and other organic matter from adjacent land.
   b. photosynthesis by phytoplankton.
   c. photosynthesis by floating aquatic plants.
   d. the activity of chemoautotrophic bacteria.
   e. minerals from the underlying bedrock.
9. During the spring overturn in a temperate zone lake:
   a. oxygen is carried from the surface to the bottom, and nutrients are carried from the bottom to the surface.
   b. nutrients are carried from the surface to the bottom, and oxygen is carried from the bottom to the surface.
   c. nutrients and oxygen are carried from the bottom waters to the surface waters.
   d. nutrients and oxygen are carried from the surface waters to the bottom waters.
   e. oxygen concentration remains constant at all depths, and nutrients sink to the bottom.
10. In which habitat must organisms adjust regularly to changing salinity?
    a. salt marsh
    b. coral reef
    c. benthic province
    d. estuary
    e. riffle

## Questions for Discussion

1. Temperate grassland and chaparral often burn in lightning-induced fires, which stimulate the germination of seeds and regrowth of existing vegetation. Do you think that companies or the government should sell fire insurance to people who build expensive homes in places where periodic fires are virtually inevitable?
2. Boreal forests generally harbor many fewer species of trees than tropical forests do. Develop three hypotheses to explain this pattern. What data would you collect to test your hypotheses?
3. Describe the biome in which you live, noting the prevailing climate and microclimates and any other factors that govern the characteristics of the organisms that naturally occur there.
4. Many regions on Earth have been developed for agriculture, industry, and human habitation. Have our activities created new biomes? What physical environments are created by development, and what plants and animals occupy developed areas?

## Experimental Analysis

Design an experiment to test the hypothesis that streams receive much of their nutrients and energy from material that falls into them from overhanging vegetation.

## Evolution Link

If the geographical ranges of species change in response to global warming, what new selection pressures will organisms face as they move into ecological communities where they have not previously occurred? Your answer should address the effects of novel species interactions as well as the effects of encountering different physical environments.

## How Would You Vote?

We cannot stop an El Niño from happening, but we might be able to minimize its environmental, social, and economic impacts. Would you support the use of taxpayer dollars to fund research into the causes and effects of El Niño? Go to www.thomsonedu.com/login to investigate both sides of the issue and then vote.