40

Population Ecology and the Distribution of Organisms

KEY CONCEPTS

40.1 Earth's climate influences the structure and distribution of terrestrial biomes

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

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

40.4 Dynamic biological processes influence population density, dispersion, and demographics

40.5 The exponential and logistic models describe the growth of populations

40.6 Population dynamics are influenced strongly by life history traits and population density

▼ **Figure 40.1** What threatens this amphibian's survival?

OVERVIEW

Discovering Ecology

When University of Delaware undergraduate Justin Yeager spent his summer abroad in Costa Rica, all he wanted was to see the tropical rain forest and to practice his Spanish. Instead, he discovered a population of the variable harlequin toad (*Atelopus varius*), a species thought to be extinct in the mountain slopes of Costa Rica and Panama, where it once lived **(Figure 40.1)**. During the 1980s and 1990s, roughly two-thirds of the 82 known species of harlequin toads vanished. Scientists think that a disease-causing chytrid fungus, *Batrachochytrium dendrobatidis*, contributed to many of these extinctions. Why was the fungus suddenly thriving in the rain forest? Cloudier days and warmer nights associated with global warming appear to have created an environment ideal for its success. As of early 2012, the toad species that Yeager found was surviving as a single known population of fewer than 100 individuals.

What environmental factors limit the geographic distribution of harlequin toads? How do variations in their food supply or interactions with other species, such as pathogens, affect the size of their population? Questions like these are the subject of **ecology** (from the Greek *oikos*, home, and *logos*, study), the scientific study of the interactions between organisms and the environment. As shown in **Figure 40.2**, ecological interactions occur at a hierarchy of scales from single organisms to the globe.

Ecology is a rigorous experimental science that requires a breadth of biological knowledge. Ecologists observe nature, generate hypotheses, manipulate environmental variables, and observe outcomes. Figure 40.2 provides a conceptual framework for the field of ecology as well as an organizational framework for this unit. In this chapter, we'll first consider how Earth's climate and other factors determine the location of major life zones on land and in the oceans. We'll then examine how ecologists investigate what controls the distribution of species and the density and size of populations. The next three chapters focus on community, ecosystem, and global ecology, as we explore how ecologists apply biological knowledge to predict the global consequences of human activities and to conserve Earth's biodiversity.

▼ Figure 40.2 Exploring the Scope of Ecological Research

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

Global Ecology

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

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

Landscape Ecology

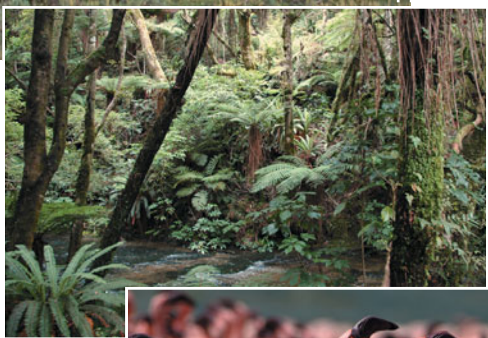
A **landscape** (or seascape) is a mosaic of connected ecosystems. Research in **landscape ecology** focuses on the factors controlling exchanges of energy, materials, and organisms across multiple ecosystems.

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

Ecosystem Ecology

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

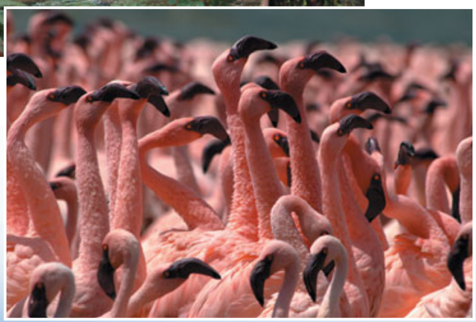
◀ What factors control photosynthetic productivity in a temperate grassland ecosystem?



Community Ecology

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

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



Population Ecology

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

◀ What environmental factors affect the reproductive rate of flamingos?

Organismal Ecology

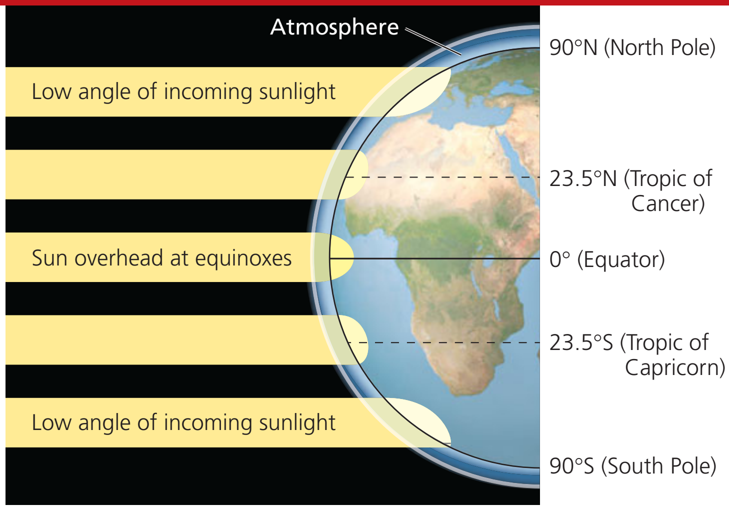
Organismal ecology, which includes the subdisciplines of physiological, evolutionary, and behavioral ecology, is concerned with how an organism's structure, physiology, and behavior meet the challenges posed by its environment.

◀ How do hammerhead sharks select a mate?

▼ Figure 40.3 **Exploring Global Climate Patterns**

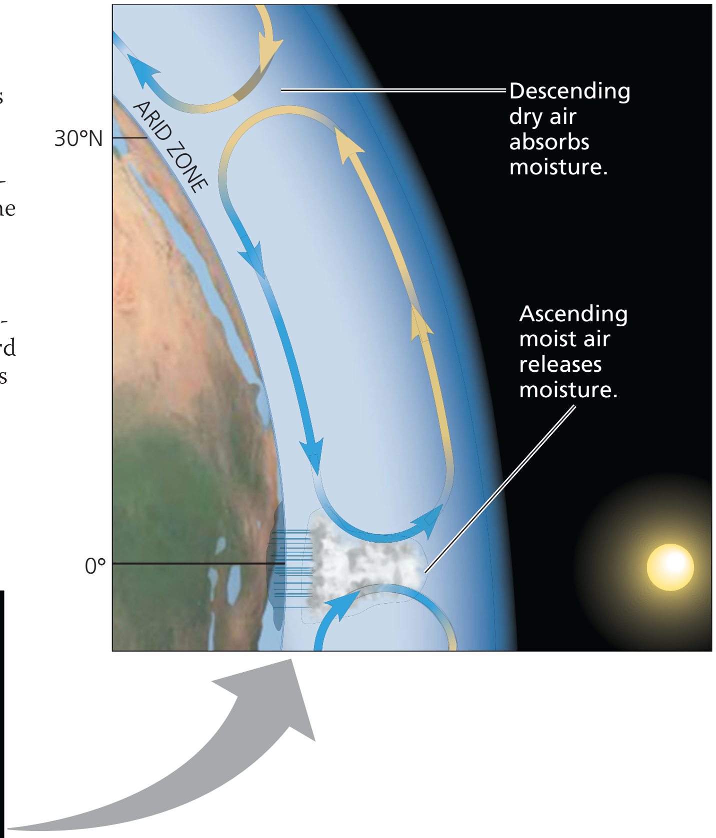
Latitudinal Variation in Sunlight Intensity

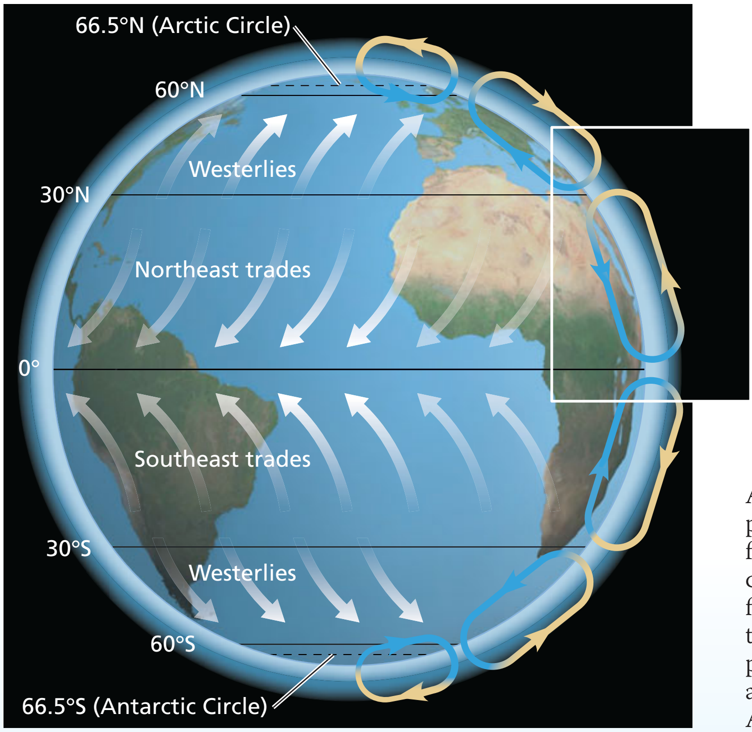
Earth's curved shape causes latitudinal variation in the intensity of sunlight. Because sunlight strikes the **tropics** (those regions that lie between 23.5° north latitude and 23.5° south latitude) most directly, more heat and light per unit of surface area are delivered there. At higher latitudes,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



Global Air Circulation and Precipitation Patterns

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





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

CONCEPT 40.1

Earth's climate influences the structure and distribution of terrestrial biomes

The most significant influence on the distribution of organisms on land and in the oceans is **climate**, the long-term, prevailing weather conditions in a given area. Four physical factors—temperature, precipitation, sunlight, and wind—are particularly important components of climate. Such **abiotic**, or nonliving, factors are the chemical and physical attributes of the environment that influence the distribution and abundance of organisms. **Biotic**, or living, factors—the other organisms that are part of an individual's environment—similarly influence the distribution and abundance of life.

We begin by describing patterns in **macroclimate**, which is climate at the global, regional, and landscape levels.

Global Climate Patterns

Global climate patterns are determined largely by the input of solar energy and Earth's movement in space. The sun warms the atmosphere, land, and water. This warming establishes the temperature variations, cycles of air and water movement, and evaporation of water that cause dramatic latitudinal variations in climate. **Figure 40.3** summarizes Earth's climate patterns and how they are formed.

Regional Effects on Climate

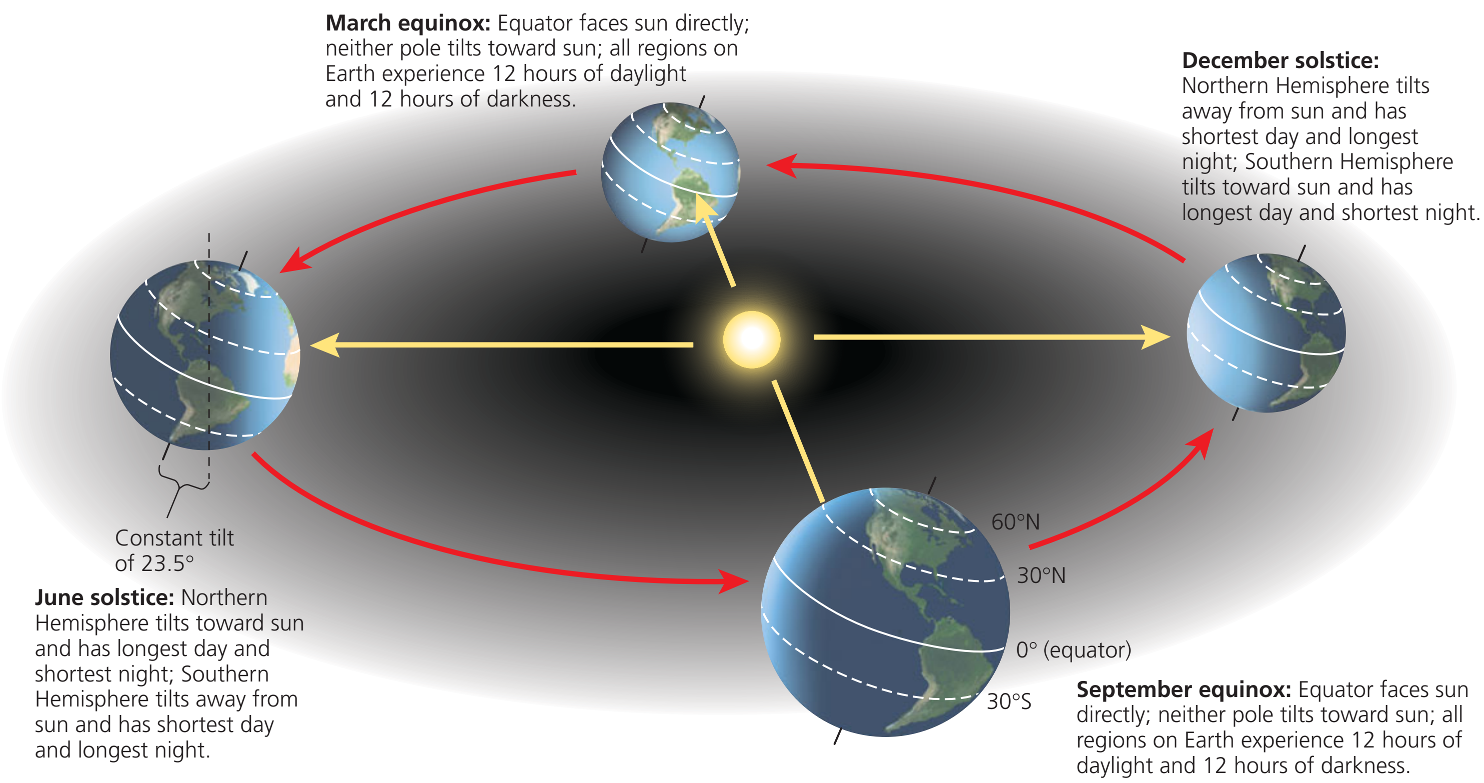
Climate patterns include seasonal variation and can be modified by other factors, such as large bodies of water and mountain ranges.

Seasonality

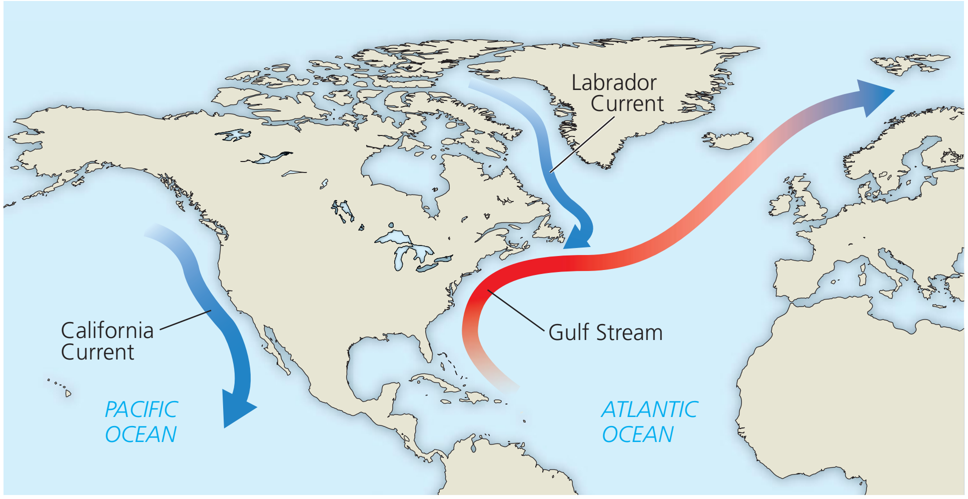
As described in **Figure 40.4**, Earth's tilted axis of rotation and its annual passage around the sun cause strong seasonal cycles in middle to high latitudes. In addition to global changes in day length, solar radiation, and temperature, the changing angle of the sun over the course of the year affects local environments. For example, the belts of wet and dry air on either side of the equator move slightly northward and southward with the changing angle of the sun, producing marked wet and dry seasons around 20° north and 20° south latitude, where many tropical deciduous forests grow. In addition, seasonal changes in wind patterns alter ocean currents, sometimes causing the upwelling of cold water from deep ocean layers. This nutrient-rich water stimulates the growth of surface-dwelling phytoplankton and the organisms that feed on them.

Bodies of Water

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



▲ **Figure 40.4 Seasonal variation in sunlight intensity.** Because Earth is tilted on its axis relative to its plane of orbit around the sun, the intensity of solar radiation varies seasonally. This variation is smallest in the tropics and increases toward the poles.



▲ **Figure 40.5 Circulation of surface water in the oceans around North America.** The California Current carries cold water southward along the western coast of North America. Along the eastern coast, the warm water of the Gulf Stream flows northward to northern Europe.

ecosystem along much of the continent's Pacific coast and large redwood groves farther south **(Figure 40.5)**. Conversely, the west coast of northern Europe has a mild climate because the Gulf Stream carries warm water from the equator to the North Atlantic. As a result, northwestern Europe is warmer during winter than southeastern Canada, which is farther south but is cooled by the Labrador Current flowing south from the coast of Greenland.

Because of the high specific heat of water (see Chapter 2), oceans and large lakes tend to moderate the climate of nearby land. During a hot day, when land is warmer than the water, air over the land heats up and rises, drawing a cool breeze from the water across the land **(Figure 40.6)**. In contrast, because temperatures drop more quickly over land than over water at night, air over the now warmer water rises, drawing cooler air from the land back out over the water and replacing it with warmer air from offshore.

Mountains

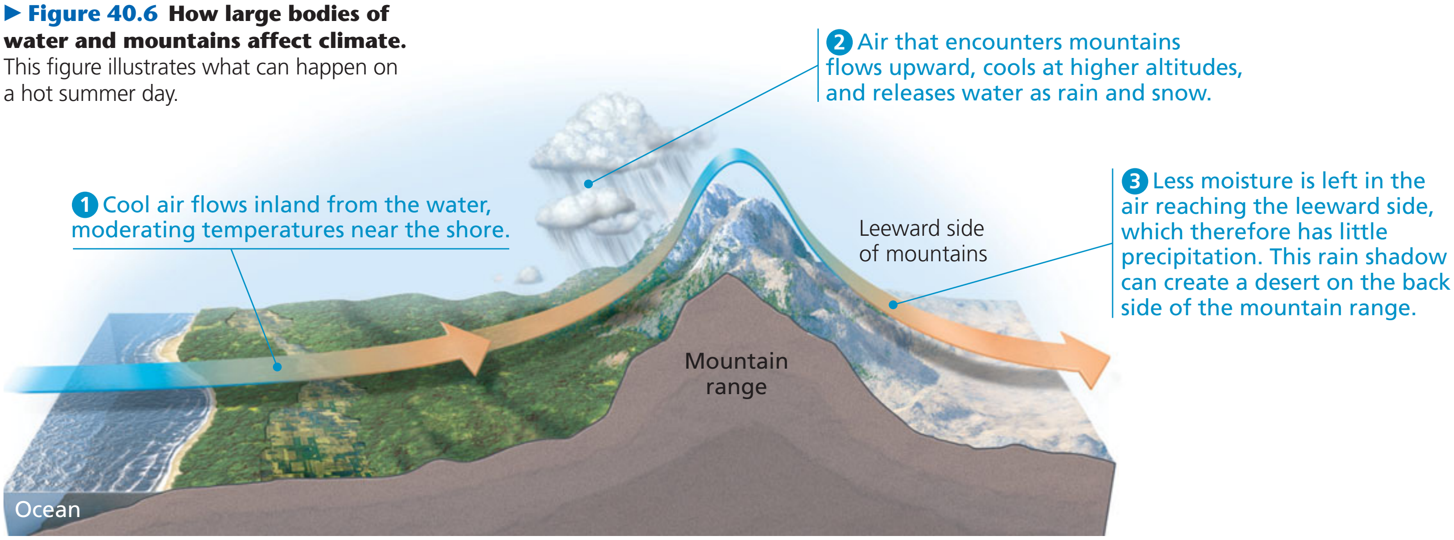
Like large bodies of water, mountains influence air flow over land. When warm, moist air approaches a mountain, the air rises and cools, releasing moisture on the windward side of the peak (see Figure 40.6). On the leeward side, cooler, dry air descends, absorbing moisture and producing a "rain shadow" that determines where many deserts are found, including the Mojave Desert of western North America and the Gobi Desert of Asia.

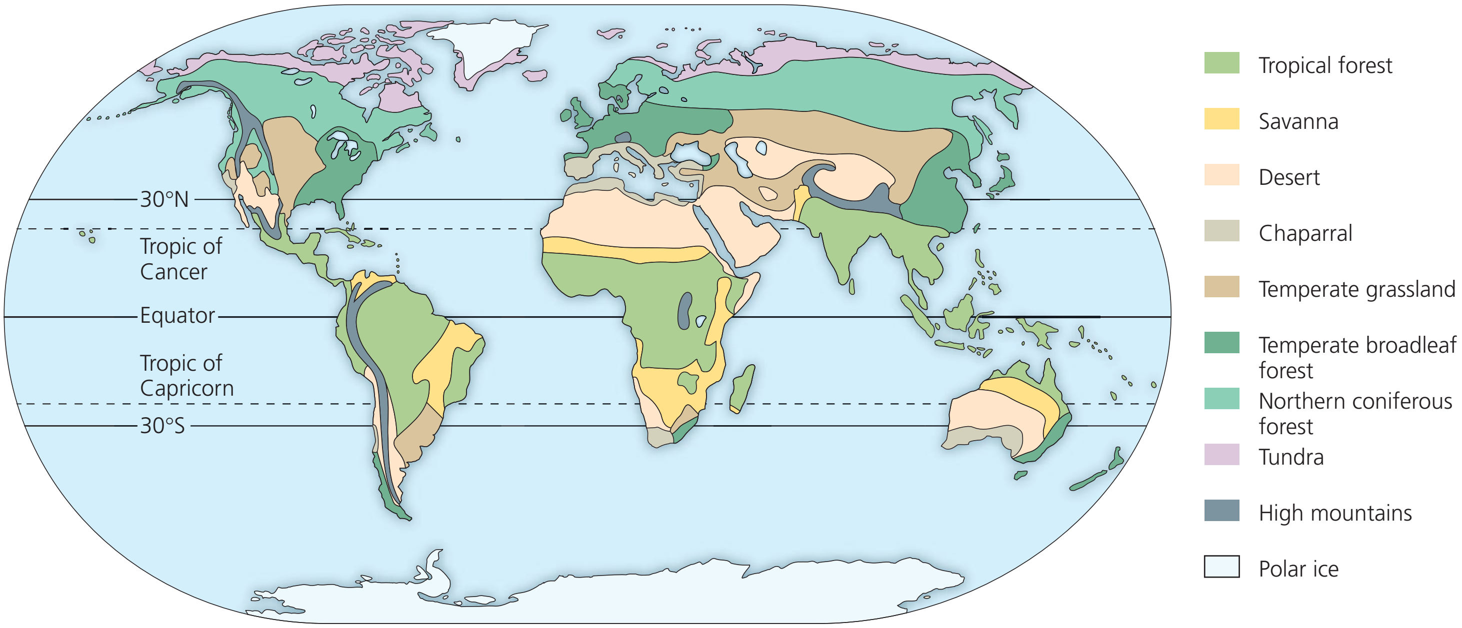
Mountains also affect the amount of sunlight reaching an area and the local temperature. South-facing slopes in the Northern Hemisphere receive more sunlight than north-facing slopes and are therefore warmer and drier. In many mountains of western North America, spruce and other conifers grow on the cooler north-facing slopes, but shrubby, drought-resistant plants inhabit the south-facing slopes. In addition, every 1,000-m increase in elevation produces an average temperature drop of approximately 6°C, equivalent to that produced by an 880-km increase in latitude. This is one reason that high-elevation communities at a given latitude can be similar to communities at lower elevations much farther from the equator.

Climate and Terrestrial Biomes

Throughout this book, you have seen examples of how climate influences where individual species are found (see Figure 8.18, for instance). We turn now to the role of climate in determining the nature and location of Earth's **biomes**, major life zones characterized by vegetation type (in terrestrial biomes) or by the physical environment (in aquatic biomes, which we will survey in Concept 40.2).

► **Figure 40.6 How large bodies of water and mountains affect climate.** This figure illustrates what can happen on a hot summer day.



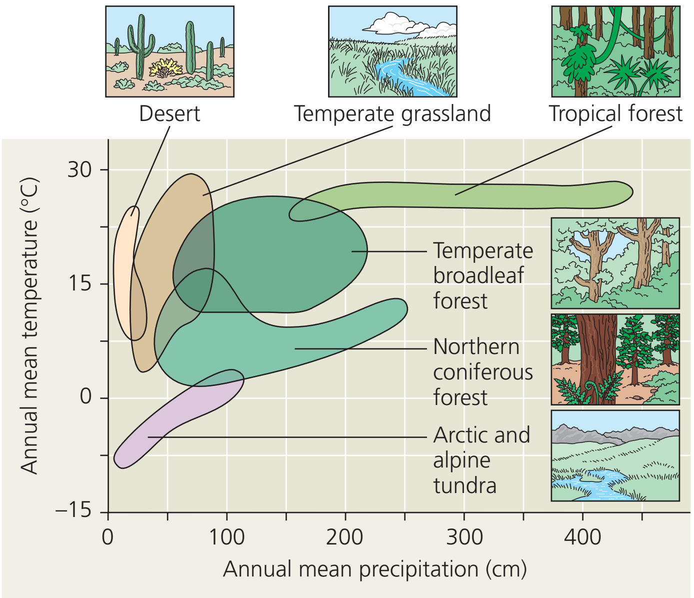


▲ **Figure 40.7 The distribution of major terrestrial biomes.** Although biomes are mapped here with sharp boundaries, biomes actually grade into one another, sometimes over large areas.

Because of the latitudinal patterns of climate described in Figure 40.3, the locations of terrestrial biomes also show strong latitudinal patterns **(Figure 40.7)**. One way to highlight the importance of climate on the distribution of biomes is to construct a **climograph**, a plot of the annual mean temperature and precipitation in a particular region **(Figure 40.8)**. Notice, for instance, that grasslands in North America are typically drier than forests and that deserts are drier still.

Factors other than mean temperature and precipitation also play a role in determining where biomes exist. For example, some areas in North America with a particular combination of temperature and precipitation support a temperate broadleaf forest, but other areas with similar values for these variables support a coniferous forest (see the overlap in Figure 40.8). One reason for this variation is that climographs are based on annual *averages*, but the *pattern* of climatic variation is often as important as the average climate. Some areas may receive regular precipitation throughout the year, whereas other areas may have distinct wet and dry seasons.

Natural and human-caused disturbances also alter the distribution of biomes. A **disturbance** is an event such as a storm, fire, or human activity that changes a community, removing organisms from it and altering resource availability. For instance, frequent fires can kill woody plants and keep a savanna from becoming the woodland that climate alone would support. Hurricanes and other storms create openings for new species in many tropical and temperate forests. Human-caused disturbances have altered much of Earth's surface, replacing natural communities with urban and agricultural ones.



▲ **Figure 40.8 A climograph for some major types of biomes in North America.** The areas plotted here encompass the ranges of annual mean temperature and precipitation in the biomes.

General Features of Terrestrial Biomes

Most terrestrial biomes are named for major physical or climatic features and for their predominant vegetation. Temperate grasslands, for instance, are generally found in middle latitudes, where the climate is more moderate than in the tropics or polar regions, and are dominated by various grass species (see Figure 40.7). Each biome is also characterized by microorganisms, fungi, and animals adapted to that particular environment. Temperate grasslands are usually more likely than temperate forests to be populated by large grazing mammals and to have arbuscular mycorrhizal fungi (see Figure 29.13).

Although Figure 40.7 shows distinct boundaries between the biomes, terrestrial biomes usually grade into each other without sharp boundaries. The area of intergradation, called an **ecotone**, may be wide or narrow.

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

Figure 40.9 summarizes the major features of terrestrial biomes.

CONCEPT CHECK 40.1

1. Explain how the sun's unequal heating of Earth's surface leads to the development of deserts around 30° north and south of the equator.
2. Identify the natural biome in which you live, and summarize its abiotic and biotic characteristics. Do these reflect your actual surroundings? Explain.
3. **WHAT IF?** If global warming increases average temperatures on Earth by 4°C in this century, predict which biome is most likely to replace tundra in some locations as a result (see Figures 40.7 and 40.8). Explain your answer.

For suggested answers, see Appendix A.

▼ Figure 40.9 Exploring Terrestrial Biomes

Tropical Forest

Distribution Equatorial and subequatorial regions

Climate Temperature is usually high, averaging 25–29°C with little seasonal variation. In **tropical rain forests**, rainfall is relatively constant, about 200–400 cm annually. In **tropical dry forests**, precipitation averages about 150–200 cm annually, with a six- to seven-month dry season.

Organisms Tropical forests are vertically layered, and plants compete strongly for light. Broadleaf evergreen trees are dominant in rain forests, whereas many dry forest trees drop their leaves during the dry season. Tropical forests are home to millions of animal species, including an estimated 5–30 million still undescribed species of insects, spiders, and other arthropods. Animal diversity is higher than in any other terrestrial biome. The animals are adapted to the vertically layered environment and are often inconspicuous.

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

A tropical rain forest in Costa Rica

A savanna in Kenya

Savanna

Distribution Equatorial and subequatorial regions

Climate Rainfall averages 30–50 cm per year in **savannas** and is seasonal, with a dry season that can last up to nine months. Temperature averages 24–29°C but varies seasonally more than in tropical forests.

Organisms Scattered trees often are thorny and have small leaves, an apparent adaptation to the relatively dry conditions. Fires are common in the dry season, and the dominant plant species are fire-adapted and tolerant of seasonal drought. Grasses and small nonwoody plants called forbs make up most of the ground cover. Large plant-eating mammals, such as wildebeests and zebras, and predators, including lions and hyenas, are common inhabitants. However, the dominant herbivores are insects, especially termites.

Human Impact The earliest humans likely lived in savannas. Overly frequent fires set by humans reduce tree regeneration by killing the seedlings and saplings. Cattle ranching and overhunting have led to declines in large-mammal populations.

Organ Pipe Cactus National Monument, Arizona

Desert

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

Climate Precipitation is low and highly variable, generally less than 30 cm per year. Temperature varies seasonally and daily. It may exceed 50°C in hot deserts and fall below −30°C in cold deserts.

Organisms Desert landscapes are dominated by low, widely scattered vegetation. Common plants include succulents such as cacti or euphorbs, deeply rooted shrubs, and herbs that grow during the infrequent moist periods. Desert plant adaptations include tolerance to heat and desiccation, water storage, reduced leaf surface area, and physical defenses such as spines and toxins in leaves. Many desert plants carry out C_4 or CAM photosynthesis. Common desert animals include scorpions, ants, beetles, snakes, lizards, migratory and resident birds, and seed-eating rodents. Many species in hot deserts are active at night, when the air is cooler. Water conservation is a common adaptation, and some animals can obtain all their water by breaking down carbohydrates in seeds.

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

Chaparral

Distribution Midlatitude coastal regions on several continents

Climate Annual precipitation is typically 30–50 cm and is highly seasonal, with rainy winters and dry summers. Fall, winter, and spring are cool, with average temperatures of 10–12°C. Average summer temperature can reach 30°C.

Organisms **Chaparral** is dominated by shrubs and small trees adapted to frequent fires. Some fire-adapted shrubs produce seeds that will germinate only after a hot fire; food reserves stored in their roots enable them to resprout quickly and use nutrients released by the fire. Adaptations to drought include tough, evergreen leaves, which reduce water loss. Animals include browsers, such as deer and goats, that feed on twigs and buds of woody vegetation; there are also many species of insects, amphibians, small mammals, and birds.

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

An area of chaparral in California

A grassland in Mongolia

Temperate Grassland

Distribution Typically at midlatitudes, often in the interior of continents

Climate Annual precipitation in **temperate grasslands** generally averages 30 to 100 cm and can be highly seasonal, with relatively dry winters and wet summers. Average temperatures frequently are below −10°C in winter and reach 30°C in summer.

Organisms Dominant plants are grasses and forbs, which vary in height from a few centimeters to 2 m in tallgrass prairie. Many grassland plants have adaptations that help them survive periodic, protracted droughts and fire. Grazing by large mammals such as bison and wild horses helps prevent establishment of woody shrubs and trees. Burrowing mammals, such as prairie dogs in North America, are also common.

Human Impact Because of their deep, fertile soils, temperate grasslands in North America and Eurasia have frequently been converted to farmland. In some drier grasslands, cattle and other grazers have turned parts of the biome into desert.

▼ **Figure 40.9** **Exploring Terrestrial Biomes**

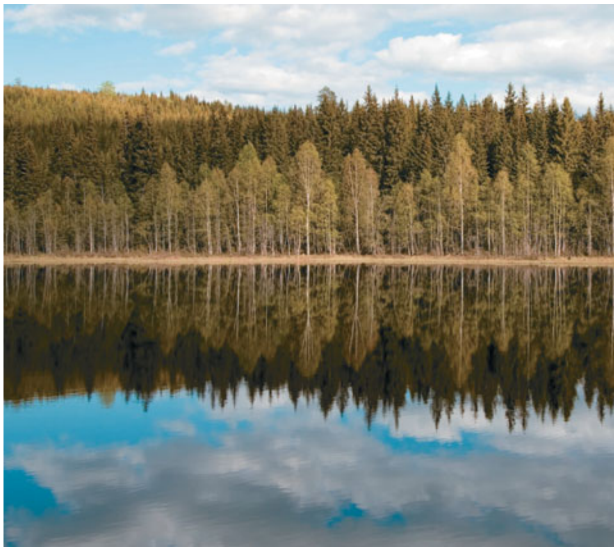
Northern Coniferous Forest

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

Climate Annual precipitation generally ranges from 30 to 70 cm. Winters are cold. Some areas of coniferous forest in Siberia typically range in temperature from −50°C in winter to over 20°C in summer.

Organisms Cone-bearing trees (conifers), such as pine, spruce, fir, and hemlock, are common, and some species depend on fire to regenerate. The conical shape of many conifers prevents snow from accumulating and breaking their branches, and their needle-like or scalelike leaves reduce water loss. Plant diversity in the shrub and herb layers is lower than in temperate broadleaf forests. Many migratory birds nest in northern coniferous forests. Mammals include moose, brown bears, and Siberian tigers. Periodic outbreaks of insects can kill vast tracts of trees.

Human Impact Although they have not been heavily settled by human populations, northern coniferous forests are being logged at a fast rate, and old-growth stands may soon disappear.



A coniferous forest in Norway

A temperate broadleaf forest in New Jersey

Temperate Broadleaf Forest

Distribution Midlatitudes in the Northern Hemisphere, with smaller areas in Chile, South Africa, Australia, and New Zealand

Climate Precipitation averages about 70 to 200 cm annually. Significant amounts fall during all seasons, with winter snow in some forests. Winter temperatures average around 0°C. Summers are humid, with maximum temperatures near 35°C.

Organisms The dominant plants of **temperate broadleaf forests** in the Northern Hemisphere are deciduous trees, which drop their leaves before winter, when low temperatures would reduce photosynthesis. In Australia, evergreen eucalyptus trees are common. In the Northern Hemisphere, many mammals hibernate in winter, while many bird species migrate to areas with warmer climates.

Human Impact Temperate broadleaf forests have been heavily settled globally. Logging and land clearing for agriculture and urban development have destroyed virtually all the original deciduous forests in North America, but these forests are returning over much of their former range.

Tundra

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

Climate Precipitation averages 20 to 60 cm annually in arctic tundra but may exceed 100 cm in alpine tundra. Winters are cold, with average temperatures in some areas below −30°C. Summer temperatures generally average less than 10°C.

Organisms The vegetation of tundra is mostly herbaceous, typically a mixture of mosses, grasses, and forbs, with some dwarf shrubs, trees, and lichens. A permanently frozen soil layer called permafrost restricts the growth of plant roots. Large grazing musk oxen are resident, while caribou and reindeer are migratory. Predators include bears, wolves, foxes, and snowy owls. Many bird species migrate to the tundra for summer nesting.

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

Dovrefjell National Park, Norway

CONCEPT 40.2

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

All types of aquatic biomes are found across the globe and show far less latitudinal variation than terrestrial biomes **(Figure 40.10)**. Ecologists distinguish between freshwater and marine biomes on the basis of physical and chemical differences. Salt concentrations generally average 3% in marine biomes but are less than 0.1% in freshwater biomes.

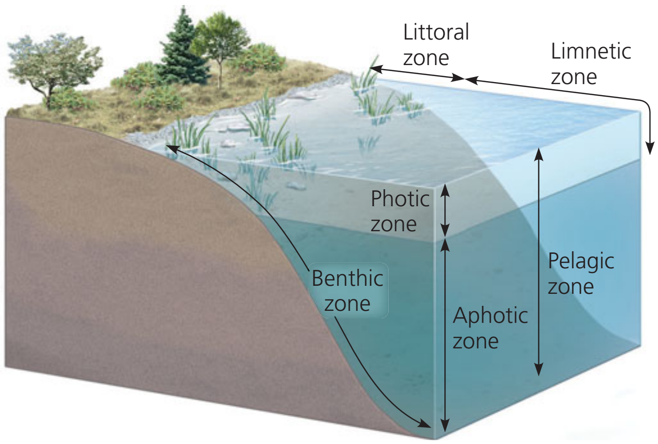
The oceans make up the largest marine biome, covering about 75% of Earth's surface. Water evaporated from the oceans provides most of the planet's rainfall, and ocean temperatures have a major effect on global climate and wind patterns (see Figure 40.3). Marine algae and photosynthetic bacteria also supply a substantial portion of the world's oxygen and consume large amounts of atmospheric carbon dioxide.

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

Zonation in Aquatic Biomes

Many aquatic biomes are divided into vertical and horizontal zones, as illustrated for a lake in **Figure 40.11**. Light is absorbed by water and by photosynthetic organisms, so its intensity decreases rapidly with depth. The upper **photic zone** is where there is sufficient light for photosynthesis, and the lower **aphotic zone** is where little light penetrates. These two zones together make up the **pelagic zone**. At the bottom of these zones, deep or shallow, is the **benthic zone**, which consists of organic and inorganic sediments and is occupied by communities of organisms called the **benthos**.

Thermal energy from sunlight warms surface waters, but the deeper waters remain cold. In the ocean and in most



▲ **Figure 40.11 Zonation in a lake.** A lake environment is generally classified on the basis of three physical criteria: light penetration (photic and aphotic zones), distance from shore and water depth (littoral and limnetic zones), and whether the environment is open water (pelagic zone) or bottom (benthic zone).

▼ **Figure 40.10 Exploring Aquatic Biomes**

Wetlands and Estuaries

Physical and Chemical Environment
Wetlands are inundated by water at least sometimes and support plants adapted to water-saturated soil. In an **estuary**, the transition zone between a river and the sea, seawater flows up and down the estuary channel during the changing tides. Nutrients from upstream make wetlands and estuaries among the most productive habitats on Earth. Because of high organic production by plants and decomposition by microorganisms, the water and soils are often low in dissolved oxygen. Both habitats filter dissolved nutrients and chemical pollutants.

Geologic Features Wetlands develop in diverse habitats, including shallow basins, the flooded banks of rivers and streams, and lake coasts. Along seacoasts, sediments from rivers and tidal waters create channels, islands, and mudflats in estuaries.

Organisms Water-saturated soils favor the growth of plants, such as cattails and sedges in wetlands and saltmarsh grasses in estuaries, that can grow in water or in soil that is anaerobic at times. In freshwater wetlands, herbivores may include crustaceans, aquatic insect larvae, and muskrats, and carnivores may include dragonflies, frogs, alligators, and herons. Estuaries support an abundance of oysters, crabs, and fish species that humans eat. Many marine invertebrates and fishes use estuaries as breeding grounds.

A basin wetland in the United Kingdom

Human Impact Draining and filling have destroyed up to 90% of wetlands. Filling, dredging, and upstream pollution have disrupted estuaries worldwide.

▼ Figure 40.10 Exploring Aquatic Biomes

Lakes

An oligotrophic lake in Alberta, Canada

Physical and Chemical Environment Standing bodies of water range from ponds a few square meters in area to lakes covering thousands of square kilometers. Light decreases with depth, creating photic and aphotic zones. Temperate lakes may have a seasonal thermocline; tropical lowland lakes have a thermocline year-round. **Oligotrophic lakes** are nutrient-poor and generally oxygen-rich; **eutrophic lakes** are nutrient-rich and often depleted of oxygen in the deepest zone in summer and if covered with ice in winter. High rates of decomposition in deeper layers of eutrophic lakes cause periodic oxygen depletion.

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

Organisms Rooted and floating aquatic plants live in the **littoral zone**, the shallow, well-lit waters close to shore. The **limnetic zone**, where water is too deep to support rooted aquatic plants, is inhabited by a variety of phytoplankton, including cyanobacteria, and small drifting heterotrophs, or zooplankton, that graze on the phytoplankton. The benthic zone is inhabited by assorted invertebrates whose species composition depends partly on oxygen levels. Fishes live in all zones with sufficient oxygen.

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

Streams and Rivers

Physical and Chemical Environment Headwater streams are generally cold, clear, turbulent, and swift. Downstream in larger rivers, the water is generally warmer and more turbid because of suspended sediment. The salt and nutrient content of streams and rivers increases from the headwaters to the mouth, but oxygen content typically decreases.

Geologic Features Headwater stream channels are often narrow, have a rocky bottom, and alternate between shallow sections and deeper pools. Rivers are generally wide and meandering. River bottoms are often silty from sediments deposited through time.

Organisms Headwater streams that flow through grasslands or deserts may be rich in phytoplankton or rooted aquatic plants. Diverse fishes and invertebrates inhabit unpolluted rivers and streams. In streams flowing through forests, organic matter from terrestrial vegetation is the primary source of food for aquatic consumers.

Human Impact Municipal, agricultural, and industrial pollution degrade water quality and can kill aquatic organisms. Dams impair the natural flow of streams and rivers and threaten migratory species such as salmon.

A headwater stream in Washington

Intertidal Zones

A rocky intertidal zone on the Oregon coast

Physical and Chemical Environment An **intertidal zone** is periodically submerged and exposed by the tides, twice daily on most marine shores. Upper strata experience longer exposures to air and greater variations in temperature and salinity, conditions that limit the distributions of many organisms to particular strata. Oxygen and nutrient levels are generally high and are renewed with each turn of the tides.

Geologic Features The rocky or sandy substrates of intertidal zones select for particular behavior and anatomy among intertidal organisms. The configuration of bays or coastlines influences the magnitude of tides and the exposure of intertidal zones to waves.

Organisms Diverse and plentiful marine algae grow on rocks in intertidal zones. Sandy intertidal zones exposed to waves generally lack attached plants or algae, while those in protected bays or lagoons often support rich beds of seagrass and algae. Some animals have structural adaptations that enable them to attach to rocks. Many animals in sandy or muddy intertidal zones, such as worms, clams, and predatory crustaceans, bury themselves and feed as the tides bring food. Other common animals are sponges, sea anemones, and small fishes.

Human Impact Oil pollution has disrupted many intertidal areas. Rock walls and barriers built to reduce erosion from waves and storm surges disrupt some areas.

Coral Reefs

A coral reef in the Red Sea

Physical and Chemical Environment **Coral reefs** are formed largely from the calcium carbonate skeletons of corals. Shallow reef-building corals live in the clear photic zone of tropical oceans, primarily near islands and along the edge of some continents. They are sensitive to temperatures below about 18–20°C and above 30°C. Deep-sea coral reefs are found at a depth of 200–1,500 m. Corals require high oxygen levels and are excluded by high inputs of fresh water and nutrients.

Geologic Features Corals require a solid substrate for attachment. A typical coral reef begins as a fringing reef on a young, high island, forms an offshore barrier reef later, and becomes a coral atoll as the older island submerges.

Organisms Unicellular algae live within the tissues of the corals in a mutualism that provides the corals with organic molecules. Diverse multicellular red and green algae also contribute substantial amounts of photosynthesis. Corals are the predominant animals on coral reefs, but fish and invertebrate diversity is also exceptionally high. Animal diversity on coral reefs rivals that of tropical forests.

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

Oceanic Pelagic Zone

Physical and Chemical Environment The **oceanic pelagic zone** is a vast realm of open blue water, whose surface is constantly mixed by wind-driven currents. Because of higher water clarity, the photic zone extends to greater depths than in coastal marine waters. Oxygen content is generally high. Nutrient levels are generally lower than in coastal waters. Mixing of surface and deeper waters in fall and spring renews nutrients in the photic zones of temperate and high-latitude ocean areas.

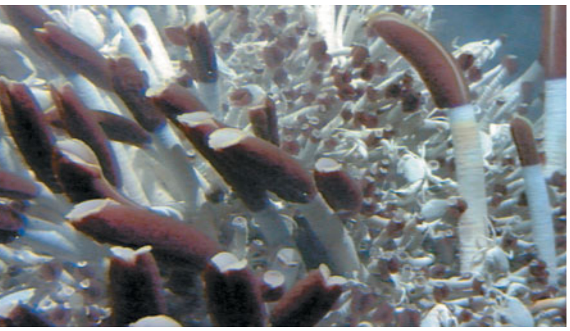
Geologic Features This biome covers approximately 70% of Earth's surface. It has an average depth of nearly 4,000 m and a maximum depth of more than 10,000 m.

Organisms The dominant photosynthetic organisms are bacteria and other phytoplankton, which drift with the currents and account for half of global productivity. Zooplankton, including protists, worms, krill, jellies, and small larvae of invertebrates and fishes, eat the phytoplankton. Free-swimming animals include large squids, fishes, sea turtles, and marine mammals.

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

Open ocean near Iceland

Marine Benthic Zone



A deep-sea hydrothermal vent community

Physical and Chemical Environment The **marine benthic zone** consists of the seafloor. Except for shallow, near-coastal areas, the marine benthic zone is dark. Water temperature declines with depth, while pressure increases. Organisms in the very deep benthic, or abyssal, zone are adapted to continuous cold (about 3°C) and high water pressure. Oxygen concentrations are generally sufficient to support diverse animal life.

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

Organisms Photosynthetic organisms, mainly seaweeds and filamentous algae, live in shallow benthic areas with sufficient light. In the dark, hot environments near **deep-sea hydrothermal vents**, the food producers are chemoautotrophic prokaryotes. Coastal benthic communities include numerous invertebrates and fishes. Below the photic zone, most consumers depend entirely on organic matter raining down from above. Among the animals of the deep-sea hydrothermal vent communities are giant tube worms (pictured at left), some more than 1 m long. They are nourished by chemoautotrophic prokaryotes that live as symbionts within their bodies. Many other invertebrates, including arthropods and echinoderms, are also abundant around the hydrothermal vents.

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

lakes, a narrow layer of abrupt temperature change called a **thermocline** separates the more uniformly warm upper layer from more uniformly cold deeper waters.

In both freshwater and marine environments, communities are distributed according to water depth, degree of light penetration, distance from shore, and whether they are found in open water or near the bottom. Plankton and many fish species live in the relatively shallow photic zone (see Figure 40.11). Most of the deep ocean is virtually devoid of light (the aphotic zone) and harbors relatively little life.

CONCEPT CHECK 40.2

The first two questions refer to Figure 40.10.

1. Why are phytoplankton, and not benthic algae or rooted aquatic plants, the dominant photosynthetic organisms of the oceanic pelagic zone?
2. **MAKE CONNECTIONS** Many organisms living in estuaries experience both freshwater and saltwater conditions each day with the rising and falling of tides. Explain how these changing conditions challenge the survival of these organisms (see Concept 32.3).
3. **WHAT IF?** Water leaving a reservoir behind a dam is often taken from deep layers of the reservoir. Would you expect fish found in a river below a dam in summer to be species that prefer colder or warmer water than fish found in an undammed river? Explain.

For suggested answers, see Appendix A.

CONCEPT 40.3

Interactions between organisms and the environment limit the distribution of species

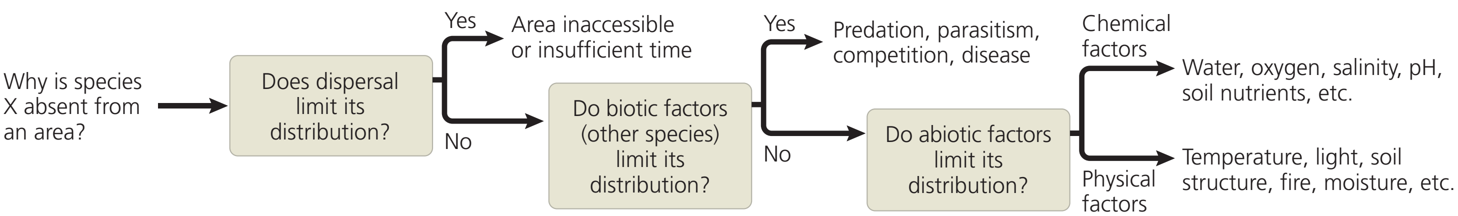
So far in this chapter, we've examined Earth's climate and the characteristics of terrestrial and aquatic biomes. We've also introduced the range of biological levels at which ecologists work (see Figure 40.2). In this section, we'll examine how ecologists determine what factors control the distribution of species, such as the harlequin toad shown in Figure 40.1.

Species distributions are a consequence of both ecological and evolutionary interactions through time. The differential survival and reproduction of individuals that lead to evolution occur in *ecological time*, the minute-to-minute time frame of interactions between organisms and the environment. Through natural selection, organisms adapt to their environment over the time frame of many generations, in *evolutionary time*. One example of how events in ecological time have led to evolution is the selection for beak depth in Galápagos finches (see Figures 21.1 and 21.2). On the island of Daphne Major, finches with larger, deeper beaks were better able to survive during a drought because they could eat the large, hard seeds that were available. Finches with shallower beaks, which required smaller, softer seeds that were in short supply, were less likely to survive and reproduce. Because beak depth is hereditary in this species, the generation of finches born after the drought had beaks that were deeper than those of previous generations.

Biologists have long recognized global and regional patterns in the distribution of organisms (see the discussion of biogeography in Chapter 19). Kangaroos, for instance, are found in Australia but nowhere else on Earth. Ecologists ask not only *where* species occur, but also *why* species occur where they do: What factors determine their distribution? Ecologists generally need to consider multiple factors and alternative hypotheses when attempting to explain the distribution of species. To see how ecologists might arrive at such an explanation, let's work our way through the series of questions in the flowchart in **Figure 40.12**.

Dispersal and Distribution

One factor that contributes greatly to the global distribution of organisms is **dispersal**, the movement of individuals or gametes away from their area of origin or from centers of high population density. A biogeographer who studies the distributions of species in the context of evolutionary theory might consider dispersal in hypothesizing why there are no kangaroos in North America: A barrier may have kept them from reaching the continent. While land-bound kangaroos have not reached North America under their own power, other organisms that disperse more readily, such as some birds, have. The dispersal of organisms is critical to understanding the role of geographic isolation in evolution (see Chapter 22) as well as the broad patterns of species distribution that we see around the world today.



▲ **Figure 40.12 Flowchart of factors limiting geographic distribution.** As ecologists study the factors limiting a species' distribution, they often consider a series of questions like the ones shown here.

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

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

Species introduced to new geographic locations often disrupt the communities and ecosystems to which they have been introduced and spread far beyond the area of introduction (see Chapter 43). Consequently, ecologists rarely move species to new geographic regions. Instead, they document the outcome when a species has been transplanted for other purposes, such as to introduce game animals or predators of pest species, or when a species has been accidentally transplanted.

Biotic Factors

If dispersal does not limit the distribution of a species, our next question is whether biotic factors—other species—are responsible. Often, negative interactions with predators (organisms that kill their prey) or herbivores (organisms that eat plants or algae) restrict the ability of a species to survive and reproduce. **Figure 40.13** describes a specific case of an herbivore, a sea urchin, limiting the distribution of a food species, a seaweed.

In addition to predation and herbivory, the presence or absence of pollinators, food resources, parasites, pathogens, or competing organisms can act as a biotic limitation on species distribution. Some of the most striking cases of limitation occur when humans accidentally or intentionally introduce exotic predators or pathogens into new areas and wipe out native species. You will encounter examples of these impacts in Chapter 43, where we discuss conservation biology.

Abiotic Factors

The last question in the flowchart in Figure 40.12 considers whether abiotic factors, such as temperature, water, oxygen, salinity, sunlight, or soil, might be limiting a species' distribution. If the physical conditions at a site do not allow a species to survive and reproduce, then the species will not be found there.

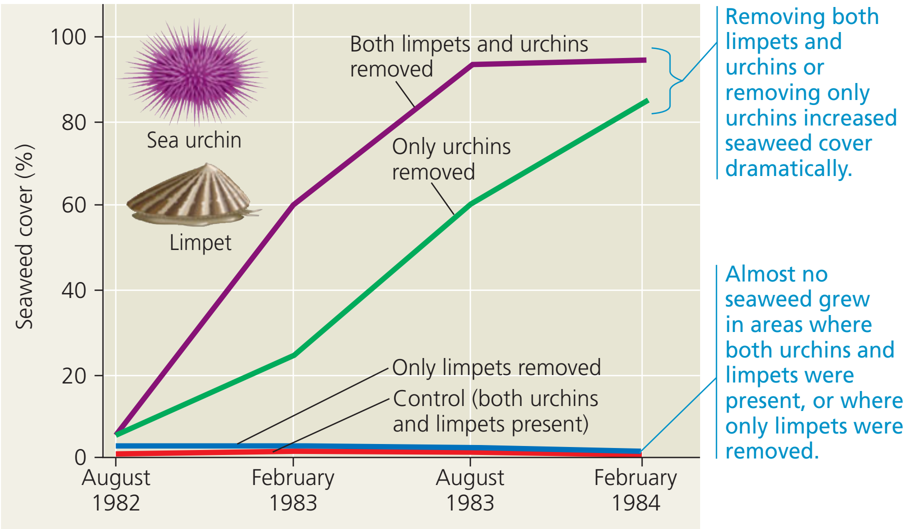
- **Temperature** Environmental temperature is an important factor in the distribution of organisms because of its effect on biological processes. Cells may rupture if the water they contain freezes (at temperatures below 0°C), and the proteins of most organisms denature at temperatures above 45°C. Most organisms function best within a specific range of environmental temperature.
- **Water and Oxygen** Variation in water availability among habitats is another important factor in species distribution. Species living at the seashore or in tidal wetlands can dry out as the tide recedes, and terrestrial organisms face a nearly constant threat of drying. Many amphibians, such as

▼ Figure 40.13 Inquiry

Does feeding by sea urchins limit seaweed distribution?

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

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



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

Source W. J. Fletcher, Interactions among subtidal Australian sea urchins, gastropods, and algae: Effects of experimental removals, *Ecological Monographs* 57:89–109 (1987).

WHAT IF? If removing only limpets did not result in an increase in seaweed growth compared to the control, suggest a reason why removing both urchins and limpets resulted in greater seaweed growth than removing only urchins.

the harlequin toad in Figure 40.1, are particularly vulnerable to drying because they use their moist, delicate skin for gas exchange.

Water affects oxygen availability in aquatic environments and in flooded soils. Because oxygen diffuses slowly in water, its concentration can be low in certain aquatic systems and soils, limiting cellular respiration and other physiological processes. Oxygen concentrations can be particularly low in both deep ocean and deep lake waters and sediments where organic matter is abundant.

- **Salinity** The salt concentration of water in the environment affects the water balance of organisms through osmosis. Most aquatic organisms are restricted to either freshwater or saltwater habitats by their limited ability to osmoregulate (see Chapter 32). Although most terrestrial organisms can excrete excess salts from specialized glands or in feces or urine, salt flats and other high-salinity habitats typically have few species of plants or animals.
- **Sunlight** Sunlight absorbed by photosynthetic organisms provides the energy that drives most ecosystems, and too little sunlight can limit the distribution of photosynthetic species. In forests, shading by leaves in the treetops makes competition for light especially intense, particularly for seedlings growing on the forest floor. In aquatic environments, most photosynthesis occurs near the surface, where sunlight is more available.
- **Rocks and Soil** On land, the pH, mineral composition, and physical structure of rocks and soil limit the distribution of plants and therefore of the animals that feed on them. The pH of soil can limit the distribution of organisms directly, through extreme acidic or basic conditions, or indirectly, by affecting the solubility of nutrients and toxins.

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

So far in this chapter, you have seen how the distributions of biomes and organisms depend on abiotic and biotic factors. In the rest of the chapter, we'll continue to work our way through the hierarchy outlined in Figure 40.2, focusing on how abiotic and biotic factors influence the ecology of populations.

CONCEPT CHECK 40.3

1. Give examples of human actions that could expand a species' distribution by changing (a) its dispersal or (b) its biotic interactions.
2. **WHAT IF?** You suspect that deer are restricting the distribution of a tree species by preferentially eating the seedlings of the tree. How might you test this hypothesis?

For suggested answers, see Appendix A.

CONCEPT 40.4

Dynamic biological processes influence population density, dispersion, and demographics

Population ecology explores how biotic and abiotic factors influence the density, distribution, and size of populations. A population is a group of individuals of a single species living in the same general area. Members of a population rely on the same resources, are influenced by similar environmental factors, and are likely to interact and breed with one another. Populations evolve as natural selection acts on heritable variations among individuals, changing the frequencies of alleles and traits over time. Evolution remains a central theme as we view populations in the context of ecology.

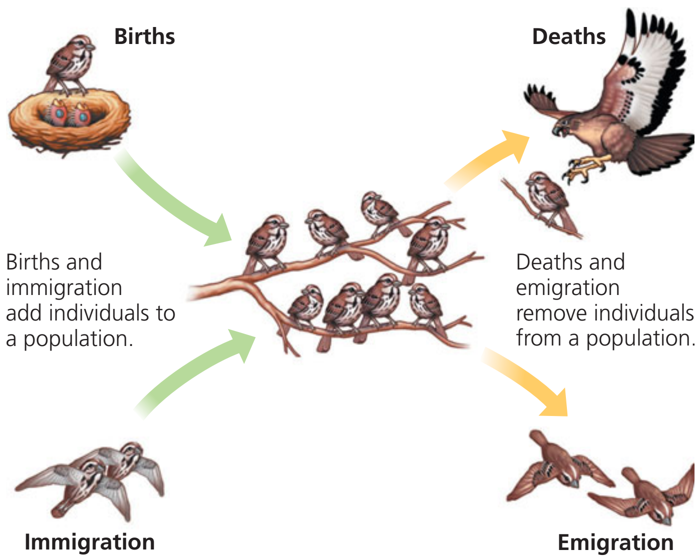
Populations are often described by their boundaries and size (number of individuals). Ecologists investigating a population define boundaries appropriate to the organism and to the questions being asked. A population's boundaries may be natural ones, as in the case of kangaroos in Australia, or they may be arbitrarily defined by an investigator—for example, a specific county in Minnesota for a study of oak trees.

Density and Dispersion

The **density** of a population is the number of individuals per unit area or volume: the number of oak trees per square kilometer in the Minnesota county or the number of bacteria per milliliter in a culture. **Dispersion** is the pattern of spacing among individuals within the boundaries of the population.

Density: A Dynamic Perspective

In rare cases, population size and density can be determined by counting all individuals within the boundaries of the population.



▲ **Figure 40.14 Population dynamics.**

We could count all the sea stars in a tide pool, for instance. Large mammals that live in herds, such as elephants, can sometimes be counted accurately from airplanes. In most cases, however, it is impractical or impossible to count all individuals in a population. Instead, ecologists use a variety of sampling techniques to estimate densities and total population sizes. For example, they might count the number of oak trees in several randomly located 100 × 100 m plots, calculate the average density in the plots, and then extend the estimate to the population size in the entire area. Such estimates are most accurate when there are many sample plots and when the habitat is fairly homogeneous. In other cases, instead of counting single organisms, population ecologists estimate density from an indicator of population size, such as the number of nests, burrows, tracks, or fecal droppings.

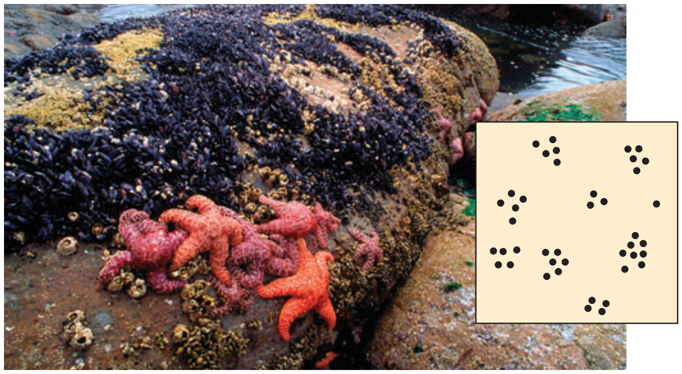
Density is not a static property but changes as individuals are added to or removed from a population **(Figure 40.14)**. Additions occur through birth (which we define here to include all forms of reproduction) and **immigration**, the influx of new individuals from other areas. The factors that remove individuals from a population are death (mortality) and **emigration**, the movement of individuals out of a population and into other locations.

While birth and death rates influence the density of all populations, immigration and emigration also alter the density of many populations. Long-term studies of Belding's ground squirrels (*Spermophilus beldingi*) in the vicinity of Tioga Pass, in the Sierra Nevada of California, showed that some of the squirrels moved nearly 2 km from where they were born. This long-distance movement made them immigrants to other populations. In fact, immigrants made up 1–8% of the males and 0.7–6% of the females in the study population. Such immigration is a meaningful biological exchange between populations over time.

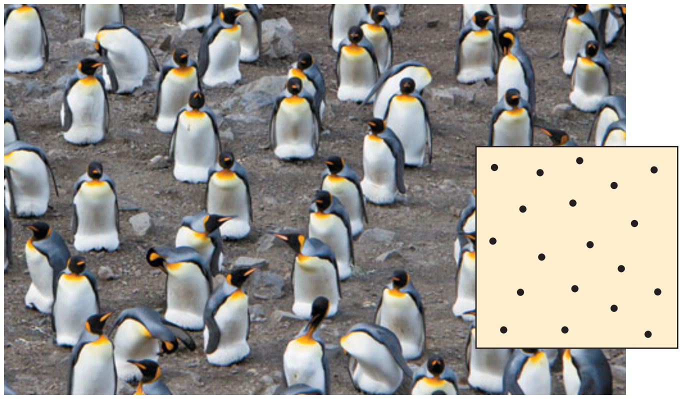
Patterns of Dispersion

Within a population's geographic range, local densities may differ substantially, creating contrasting patterns of dispersion. Differences in local density are among the most important characteristics for a population ecologist to study, since they provide insight into the environmental associations and social interactions of individuals in the population.

The most common pattern of dispersion is *clumped*, in which individuals are aggregated in patches. Plants and fungi are often clumped where soil conditions and other environmental factors favor germination and growth. Insects and salamanders may be clumped under a rotting log because of the higher humidity there. Clumping of animals may also be associated with mating behavior. Sea stars group together in tide pools, where food is readily available and where they can breed successfully **(Figure 40.15a)**. Forming groups may also increase the effectiveness of predation or defense; for example, a wolf pack is more likely than a single wolf to subdue a moose, and a flock of birds is more likely than a single bird to warn of a potential attack.



(a) Clumped. Sea stars group together where food is abundant.



(b) Uniform. Nesting king penguins exhibit uniform spacing, maintained by aggressive interactions between neighbors.

(c) Random. Dandelions grow from windblown seeds that land at random and later germinate.

▲ **Figure 40.15 Patterns of dispersion within a population's geographic range.**

A *uniform*, or evenly spaced, pattern of dispersion may result from direct interactions between individuals in the population. Some plants secrete chemicals that inhibit the germination and growth of nearby individuals that could compete for resources. Animals often exhibit uniform dispersion as a result of antagonistic social interactions, such as **territoriality**—the defense of a bounded physical space against encroachment by other individuals **(Figure 40.15b)**. Uniform patterns are rarer than clumped patterns.

In *random* dispersion (unpredictable spacing), the position of each individual in a population is independent of other individuals. This pattern occurs in the absence of strong attractions or repulsions among individuals or where key physical or chemical factors are relatively constant across the study area. Plants established by windblown seeds, such as dandelions, may be randomly distributed in a fairly uniform habitat **(Figure 40.15c)**.

Demographics

The factors that influence population density and dispersion patterns—ecological needs of a species, structure of the environment, and interactions among individuals within the population—also influence other characteristics of populations. **Demography** is the study of the vital statistics of populations and how they change over time. Of particular interest to demographers are birth rates and death rates. A useful way to summarize some of the vital statistics of a population is to make a life table.

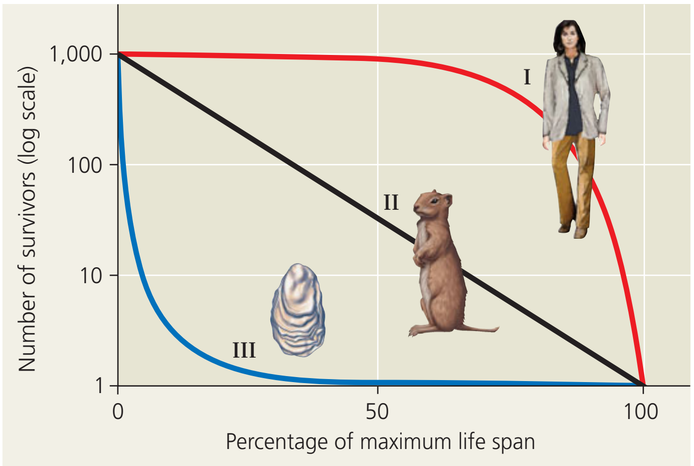
Life Tables

About a century ago, when life insurance first became available, insurance companies began to estimate how long, on average, people of a given age could be expected to live. To do this, demographers developed **life tables**, age-specific summaries of the survival pattern of a population. Population ecologists adapted this approach to the study of populations in general.

The best way to construct a life table is to follow the fate of a **cohort**, a group of individuals of the same age, from birth until all of the individuals are dead. To build the life table, we need to determine the number of individuals that die in each age-group and to calculate the proportion of the cohort surviving from one age class to the next.

Survivorship Curves

A graphic method of representing some of the data in a life table is a **survivorship curve**, a plot of the proportion or numbers in a cohort still alive at each age. Generally, a survivorship curve begins with a cohort of a convenient size—say, 1,000 individuals. Though diverse, survivorship curves can be classified into three general types **(Figure 40.16)**. A Type I curve is flat at the start, reflecting low death rates during early and middle life, and then drops steeply as death rates increase among older age-groups. Many large mammals, including humans, that produce few offspring but provide them with good care exhibit this kind of curve. In contrast, a Type III curve drops sharply at the start, reflecting very high death rates for the young, but flattens out as death rates decline for those few individuals that survive the early period of die-off. This type of curve is usually associated with organisms that produce very large numbers of offspring but provide little or no care, such as long-lived plants, many fishes, and most marine invertebrates. An oyster, for example, may release millions of eggs, but most larvae hatched from fertilized eggs die from predation or other causes. Those few offspring that survive long enough to attach to a suitable substrate and begin growing a hard shell tend to survive for a relatively long time. Type II curves are intermediate, with a constant death rate over the organism's life span. This kind of survivorship occurs in some rodents, invertebrates, lizards, and annual plants.



▲ **Figure 40.16 Idealized survivorship curves: Types I, II, and III.** The *y*-axis is logarithmic and the *x*-axis is on a relative scale so that species with widely varying life spans can be presented together on the same graph.

Many species fall somewhere between these basic types of survivorship or show more complex patterns. In birds, mortality is often high among the youngest individuals (as in a Type III curve) but fairly constant among adults (as in a Type II curve). Some invertebrates, such as crabs, may show a "stair-stepped" curve, with brief periods of increased mortality during molts, followed by periods of lower mortality when their protective exoskeleton is hard.

In populations not experiencing immigration or emigration, survivorship is one of the two key factors determining changes in population size. The other key factor determining population trends is reproductive rate.

Reproductive Rates

Demographers who study sexually reproducing species generally ignore the males and concentrate on the females in a population because only females produce offspring. Therefore, demographers view populations in terms of females giving rise to new females. The simplest way to describe the reproductive pattern of a population is to ask how reproductive output varies with the ages of females.

A **reproductive table**, or fertility schedule, is an age-specific summary of the reproductive rates in a population. It is constructed by measuring the reproductive output of a cohort from birth until death. For a sexual species, the reproductive table tallies the number of female offspring produced by each age-group. **Table 40.1** illustrates a reproductive table for Belding's ground squirrels. Reproductive output for sexual organisms such as birds and mammals is the product of the

Table 40.1 Reproductive Table for Belding's Ground Squirrels at Tioga Pass

Age (years)	Proportion of Females Weaning a Litter	Mean Size of Litters (Males + Females)	Mean Number of Females in a Litter	Average Number of Female Offspring*
0–1	0.00	0.00	0.00	0.00
1–2	0.65	3.30	1.65	1.07
2–3	0.92	4.05	2.03	1.87
3–4	0.90	4.90	2.45	2.21
4–5	0.95	5.45	2.73	2.59
5–6	1.00	4.15	2.08	2.08
6–7	1.00	3.40	1.70	1.70
7–8	1.00	3.85	1.93	1.93
8–9	1.00	3.85	1.93	1.93
9–10	1.00	3.15	1.58	1.58

Source P. W. Sherman and M. L. Morton, Demography of Belding's ground squirrel, *Ecology* 65:1617–1628 (1984).

*The average number of female offspring is the proportion weaning a litter multiplied by the mean number of females in a litter.

proportion of females of a given age that are breeding and the number of female offspring of those breeding females. Multiplying these numbers gives the average number of female offspring for each female in a given age-group (the last column in Table 40.1). For Belding's ground squirrels, which begin to reproduce at age 1 year, reproductive output rises to a peak at 4 years of age and then falls off in older females.

Reproductive tables vary considerably by species. Squirrels, for example, have a litter of two to six young once a year for less than a decade, whereas oak trees may drop thousands of acorns a year for hundreds of years. Mussels and other invertebrates may release millions of eggs and sperm in a spawning cycle. However, a high reproductive rate will not lead to rapid population growth unless conditions are near ideal for the growth and survival of offspring, as you'll learn in the next section.

CONCEPT CHECK 40.4

1. **DRAW IT** Each female of a particular fish species produces millions of eggs per year. Draw and label the most likely survivorship curve for this species, and explain your choice.
2. Imagine that you are constructing a life table for a different population of Belding's ground squirrels than the one shown in Table 40.1. If the proportion of females aged 5–6 years weaning a litter is 0.74 and the mean number of females in a litter is 3.01, what is the average number of female offspring for this cohort in a year?
3. **MAKE CONNECTIONS** A male stickleback fish attacks other males that invade its nesting territory (see Figure 39.15a). Predict the likely pattern of dispersion for male sticklebacks, and explain your reasoning.

For suggested answers, see Appendix A.

CONCEPT **40.5**

The exponential and logistic models describe the growth of populations

Populations of all species have the potential to expand greatly when resources are abundant. To appreciate the potential for population increase, consider a bacterium that can reproduce by fission every 20 minutes under ideal laboratory conditions. There would be two bacteria after 20 minutes, four after 40 minutes, and eight after 60 minutes. If reproduction continued at this rate for a day and a half without mortality, there would be enough bacteria to form a layer 30 cm deep over the entire globe. Unlimited growth cannot occur for long in nature, however. As population density increases, each individual has access to fewer resources. Ecologists study population growth in idealized conditions and in the more realistic conditions where different factors limit growth. We'll examine both scenarios in this section.

Per Capita Rate of Increase

Imagine a population consisting of a few individuals living in an ideal, unlimited environment. Under these conditions, there are no external limits on the abilities of individuals to harvest energy, grow, and reproduce. The population will increase in size with every birth and with the immigration of individuals from other populations, and it will decrease in size with every death and with the emigration of individuals out of the population. We can thus define a change in population size during a fixed time interval with the following verbal equation:

$$\text{Change in population size} = \text{Births} + \text{Immigrants entering population} - \text{Deaths} - \text{Emigrants leaving population}$$

For now, we will simplify the equation by ignoring the effects of immigration and emigration.

We can use mathematical notation to express our simplified equation more concisely. If N represents population size and t represents time, then ΔN is the change in population size and Δt is the time interval (appropriate to the life span or generation time of the species) over which we are evaluating population growth. (The Greek letter delta, Δ, indicates change, such as change in time.) Using B for the number of births in the population during the time interval and D for the number of deaths, we can rewrite the verbal equation:

$$\frac{\Delta N}{\Delta t} = B - D$$

Next, we can convert this simple model to one in which births and deaths are expressed as the average number of births and deaths per individual (per capita) during the specified time interval. The *per capita birth rate* is the number of offspring produced per unit time by an average member of the population. If, for example, there are 34 births per year in a population of 1,000 individuals, the annual per capita birth rate is 34/1,000, or 0.034. If we know the annual per capita birth rate (symbolized by b), we can use the formula $B = bN$ to calculate the expected number of births per year in a population of any size. For example, if the annual per capita birth rate is 0.034 and the population size is 500,

$$B = bN = 0.034 \times 500 = 17 \text{ per year}$$

Similarly, the *per capita death rate* (symbolized by m, for mortality) allows us to calculate the expected number of deaths per unit time in a population, using the formula $D = mN$. If $m = 0.016$ per year, we would expect 16 deaths per year in a population of 1,000 individuals. The per capita birth and death rates can be calculated from estimates of population size and data in life tables and reproductive tables (for example, Table 40.1).

Now we can revise the population growth equation again, using per capita birth and death rates rather than the numbers of births and deaths:

$$\frac{\Delta N}{\Delta t} = bN - mN$$

One final simplification is in order. Population ecologists are most interested in the *difference* between the per capita birth rate and the per capita death rate. This difference is the *per capita rate of increase*, or r:

$$r = b - m$$

The value of r indicates whether a given population is growing ($r > 0$) or declining ($r < 0$). **Zero population growth (ZPG)** occurs when the per capita birth and death rates are equal ($r = 0$). Births and deaths still occur in such a population, of course, but they balance each other exactly.

Using the per capita rate of increase, we can now rewrite the equation for change in population size as

$$\frac{\Delta N}{\Delta t} = rN$$

Remember that this equation is for a specific time interval (often one year) and does not include immigration or emigration. Most ecologists prefer to use differential calculus to express population growth *instantaneously*:

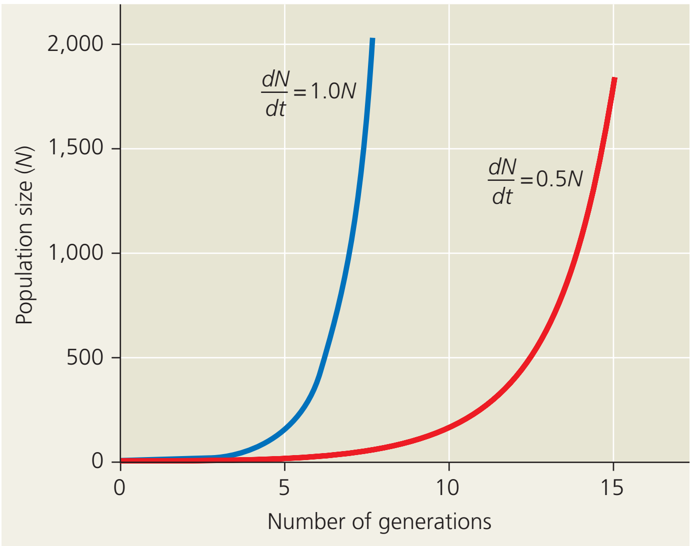
$$\frac{dN}{dt} = r_{inst}N$$

Here, r_{inst} is the instantaneous per capita rate of increase.

Exponential Growth

Earlier we described a population whose members all have access to abundant food and are free to reproduce at their physiological capacity. Population increase under these ideal conditions is called **exponential population growth**. Under these conditions, the per capita rate of increase may assume the maximum rate for the species, denoted as r_{max}. The equation for exponential population growth is

$$\frac{dN}{dt} = r_{max}N$$



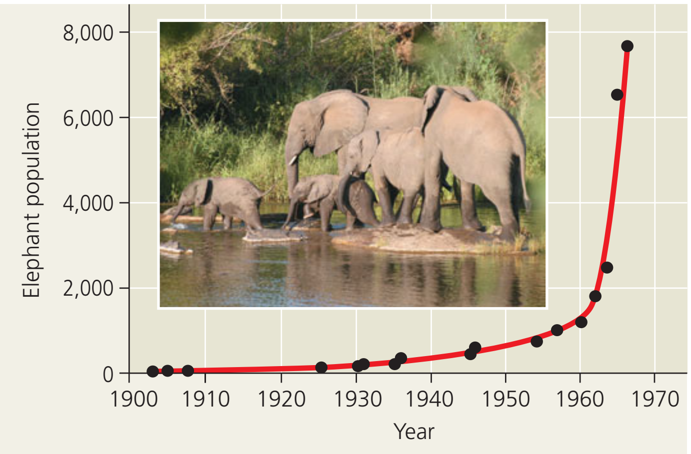
▲ **Figure 40.17 Population growth predicted by the exponential model.** This graph compares growth in two populations with different values of r_{max}. Increasing the value of r_{max} from 0.5 to 1.0 increases the rate of rise in population size over time, as reflected by the relative slopes of the curves at any given population size.

The size of a population that is growing exponentially increases at a constant rate, resulting eventually in a J-shaped growth curve when population size is plotted over time **(Figure 40.17)**. Although the maximum *rate* of increase is constant, the population grows more quickly when it is large than when it is small; thus, the curves in Figure 40.17 get progressively steeper over time. This occurs because population growth depends on N as well as r_{max}, and larger populations experience more births (and deaths) than small ones growing at the same per capita rate. It is also clear from Figure 40.17 that a population with a higher maximum rate of increase ($dN/dt = 1.0N$) will grow faster than one with a lower rate of increase ($dN/dt = 0.5N$).

The J-shaped curve of exponential growth is characteristic of some populations that are introduced into a new environment or whose numbers were drastically reduced and are rebounding. For example, the population of elephants in Kruger National Park, South Africa, grew exponentially for approximately 60 years after they were first protected from hunting **(Figure 40.18)**. The increasing number of elephants eventually caused enough damage to vegetation in the park that a collapse in their food supply was likely. To protect other species and the ecosystem before that happened, park managers began limiting the elephant population by using birth control and exporting elephants to other countries.

Carrying Capacity

The exponential growth model assumes that resources are unlimited, which is rarely the case in the real world. Ultimately, there is a limit to the number of individuals that can occupy a habitat. Ecologists define **carrying capacity**, symbolized by K,



▲ Figure 40.18 Exponential growth in the African elephant population of Kruger National Park, South Africa.

Table 40.2 Logistic Growth of a Hypothetical Population ($K = 1{,}500$)

Population Size (N)	Maximum Rate of Increase (r_{max})	$\frac{K-N}{K}$	Per Capita Rate of Increase $r_{max}\frac{(K-N)}{K}$	Population Growth Rate* $r_{max}N\frac{(K-N)}{K}$
25	1.0	0.98	0.98	+25
100	1.0	0.93	0.93	+93
250	1.0	0.83	0.83	+208
500	1.0	0.67	0.67	+333
750	1.0	0.50	0.50	+375
1,000	1.0	0.33	0.33	+333
1,500	1.0	0.00	0.00	0

*Rounded to the nearest whole number.

as the maximum population size that a particular environment can sustain. Carrying capacity varies over space and time with the abundance of limiting resources. Energy, shelter, refuge from predators, nutrient availability, water, and suitable nesting sites can all be limiting factors. For example, the carrying capacity for bats may be high in a habitat with abundant flying insects and roosting sites, but lower where there is abundant food but fewer suitable shelters.

Crowding and resource limitation can have a profound effect on population growth rate. If individuals cannot obtain sufficient resources to reproduce, the per capita birth rate (b) will decline. If they cannot consume enough energy to maintain themselves or if disease increases with density, the per capita death rate (m) may increase. A decrease in b or an increase in m lowers the per capita rate of increase (r).

The Logistic Growth Model

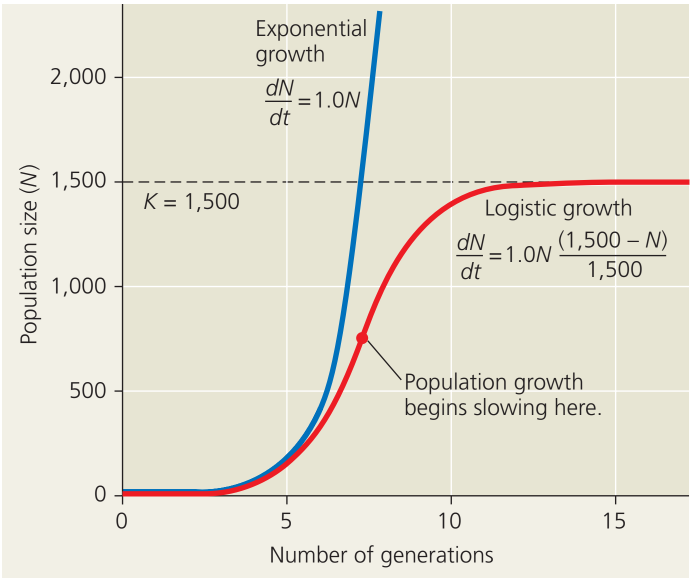
We can modify our mathematical model to include changes in growth rate as N increases. In the **logistic population growth** model, the per capita rate of increase approaches zero as the population size nears its carrying capacity.

To construct the logistic model, we start with the exponential population growth model and add an expression that reduces the per capita rate of increase as N increases. If the maximum sustainable population size (carrying capacity) is K, then $K - N$ is the number of additional individuals the environment can support, and $(K - N)/K$ is the fraction of K that is still available for population growth. By multiplying the exponential rate of increase $r_{max}N$ by $(K - N)/K$, we modify the change in population size as N increases:

$$\frac{dN}{dt} = r_{max}N\frac{(K-N)}{K}$$

When N is small compared with K, the term $(K - N)/K$ is close to 1, and the per capita rate of increase, $r_{max}(K - N)/K$, approaches the maximum rate of increase. But when N is large and resources are limiting, then $(K - N)/K$ is close to 0, and the per capita rate of increase is small. When N equals K, the population stops growing. **Table 40.2** shows calculations of population growth rate for a hypothetical population growing according to the logistic model, with $r_{max} = 1.0$ per individual per year. Notice that the overall population growth rate is highest, +375 individuals per year, when the population size is 750, or half the carrying capacity. At a population size of 750, the per capita rate of increase remains relatively high (one-half the maximum rate), but there are more reproducing individuals (N) in the population than at lower population sizes.

As shown in **Figure 40.19**, the logistic model of population growth produces a sigmoid (S-shaped) growth curve when N



▲ Figure 40.19 Population growth predicted by the logistic model. The rate of population growth decreases as population size (N) approaches the carrying capacity (K) of the environment. The red line shows logistic growth in a population where $r_{max} = 1.0$ and $K = 1{,}500$ individuals. For comparison, the blue line illustrates a population continuing to grow exponentially with the same r_{max}.

Scientific Skills Exercise

Using the Logistic Equation to Model Population Growth

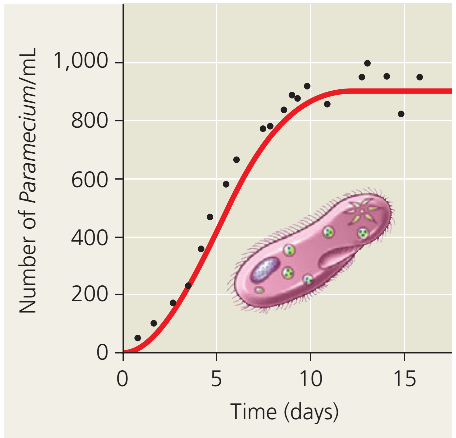
What Happens to the Size of a Population When It Overshoots Its Carrying Capacity? In the logistic population growth model, the per capita rate of population increase approaches zero as the population size (*N*) approaches the carrying capacity (*K*). Under some conditions, however, a population in the laboratory or the field can overshoot *K*, at least temporarily. For instance, if food becomes limiting to a population, there may be a delay before reproduction declines, and *N* may briefly exceed *K*. In this exercise, you will use the logistic equation to model the growth of the hypothetical population in Table 40.2 when $N > K$.

Interpret the Data

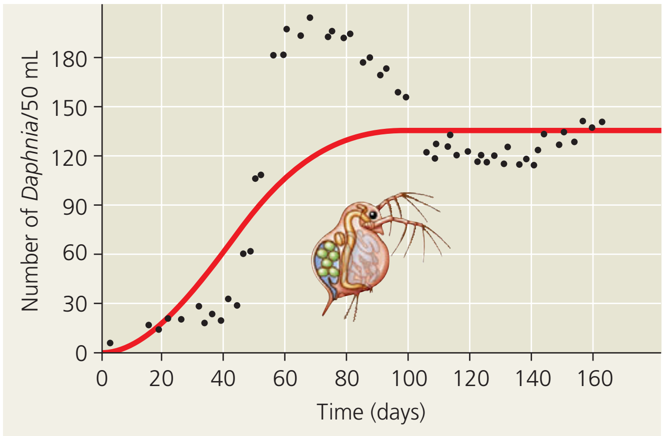
1. Assuming that r_{max}=1.0 and K = 1,500, calculate the population growth rate for four cases where population size (*N*) is greater than carrying capacity (*K*): N=1,510; 1,600; 1,750; and 2,000 individuals. To do this, first write the equation for population growth rate given in Table 40.2. Plug in the values for each of the four cases, starting with N=1,510, and solve the equation for each one. Which population size has the highest growth rate?
2. If r_{max} is doubled, predict how the population growth rates will change for the four population sizes given in question 1. Now calculate the population growth rate for the same four cases, this time assuming that r_{max}= 2.0 (and *K* still = 1,500).
3. Now let's see how the growth of a real-world population of *Daphnia* corresponds to this model. At what times in Figure 40.20b is the *Daphnia* population changing in ways that correspond to the values you calculated? Hypothesize why the population drops below the carrying capacity briefly late in the experiment.

MB A version of this Scientific Skills Exercise can be assigned in MasteringBiology.

▶ Figure 40.20
How well do these populations fit the logistic growth model? In each graph, the black dots plot the measured growth of the population, and the red curve is the growth predicted by the logistic model.



(a) A *Paramecium* population in the lab. Growth in a small culture closely approximates logistic growth if the researcher maintains a constant environment.



(b) A *Daphnia* (water flea) population in the lab. Growth in a small culture does not correspond well to the logistic model. This population overshoots the carrying capacity of its artificial environment before reaching an approximately stable size.

is plotted over time (the red line). New individuals are added to the population most rapidly at intermediate population sizes, when there is not only a breeding population of substantial size, but also lots of available space and other resources in the environment. The population growth rate decreases dramatically as *N* approaches *K*.

Note that we haven't said anything yet about *why* the population growth rate decreases as *N* approaches *K*. For a population's growth rate to decrease, the birth rate *b* must decrease, the death rate *m* must increase, or both. Later in this chapter, we'll consider some of the factors affecting these rates, including the presence of disease, predation, and limited amounts of food and other resources. In the **Scientific Skills Exercise**, you can model what happens to a population if *N* becomes *greater* than *K*.

The Logistic Model and Real Populations

The growth of laboratory populations of some small animals, such as beetles and crustaceans, and of some microorganisms, such as bacteria, *Paramecium*, and yeasts, fits an S-shaped curve fairly well under conditions of limited resources **(Figure 40.20a)**. These populations are grown in a constant environment lacking predators and competing species that may reduce growth of the populations, conditions that rarely occur in nature.

The assumptions built into the logistic model clearly do not apply to all populations. It assumes that populations adjust instantaneously to growth and approach carrying capacity smoothly. In reality, there is often a delay before the negative effects of an increasing population are realized. If food becomes limiting for a population, for instance, reproduction will decline eventually, but females may use their energy reserves to continue reproducing for a short time. This may cause the population to overshoot its carrying capacity temporarily, as shown for the water fleas in **Figure 40.20b**. Other populations fluctuate greatly, making it difficult even to define carrying capacity. We'll examine some possible reasons for such fluctuations later in this chapter.

The logistic model is a useful starting point for thinking about how populations grow and for constructing more complex models. The model is also important in conservation biology for predicting how rapidly a particular population might increase in numbers after it has been reduced to a small size and for estimating sustainable harvest rates for wildlife populations. Conservation biologists can use the model to estimate the critical size below which populations of certain organisms may become extinct.

CONCEPT CHECK 40.5

1. Why does a constant rate of increase (r_{max}) for a population produce a growth curve that is J-shaped?
2. Explain why a population that fits the logistic growth model increases more rapidly at intermediate size than at relatively small and large sizes.
3. **MAKE CONNECTIONS** Many viruses are pathogens of animals and plants (see Concept 17.3). How might the presence of pathogens alter the carrying capacity of a population? Explain.

For suggested answers, see Appendix A.

CONCEPT 40.6

Population dynamics are influenced strongly by life history traits and population density

EVOLUTION What environmental factors keep populations from growing indefinitely? Why are some populations fairly stable in size, while others are not? The answers to these questions depend in part on the traits of individuals, influenced through time by natural selection, and also on factors in the environment that vary with population density.

In every species, there are trade-offs between survival and reproductive traits such as frequency of reproduction, number of offspring (number of seeds produced by plants; litter or clutch size for animals), and investment in parental care. The traits that affect an organism's schedule of reproduction and survival make up its **life history**. A life history entails three main variables: when reproduction begins (the age at first reproduction or age at maturity), how often the organism reproduces, and how many offspring are produced per reproductive episode.

"Trade-offs" and Life Histories

No organism could produce unlimited numbers of offspring *and* provision them well. There is a trade-off between reproduction and survival. For instance, researchers in Scotland found that female red deer that reproduced in a given summer were more likely to die the next winter than were females that did not reproduce.

Selective pressures influence the trade-off between the number and size of offspring. Plants and animals whose young are likely to die often produce many small offspring. Plants that colonize disturbed environments, for example, usually produce many small seeds, only a few of which may reach a suitable habitat. Small size may also increase the chance of seedling establishment by enabling the seeds to be carried longer distances to a broader range of habitats **(Figure 40.21a)**. Animals that suffer high predation rates, such as quail, sardines, and mice, also tend to produce large numbers of offspring.

In other organisms, extra investment on the part of the parent greatly increases the offspring's chance of survival. Walnut and Brazil nut trees provision large seeds with nutrients that help the seedlings become established **(Figure 40.21b)**. Primates generally bear only one or two offspring at a time; parental care and an extended period of learning in the first several years of life are very important to offspring fitness. Such provisioning and extra care can be especially important in habitats with high population densities.

Ecologists have attempted to connect differences in favored traits at different population densities with the logistic growth model discussed in Concept 40.5. Selection for traits that are sensitive to population density and are favored at high densities

(a) Dandelions grow quickly and release a large number of tiny fruits, each containing a single seed. Producing numerous seeds ensures that at least some will grow into plants that eventually produce seeds themselves.

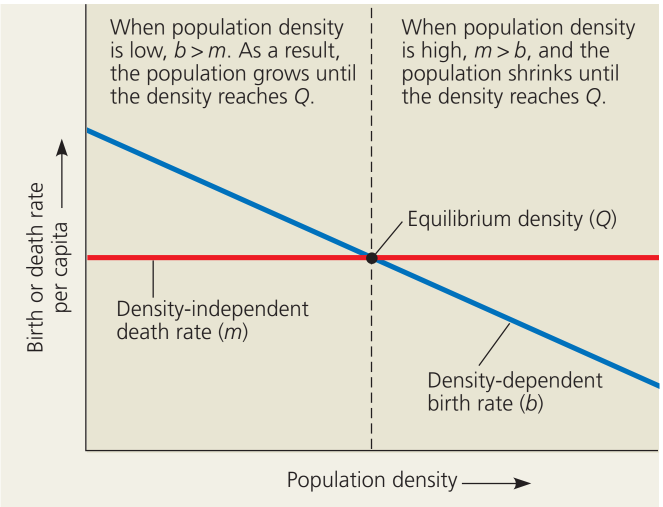
(b) Some plants, such as the Brazil nut tree (right), produce a moderate number of large seeds in pods (above). Each seed's large endosperm provides nutrients for the embryo, an adaptation that helps a relatively large fraction of offspring survive.

▲ **Figure 40.21 Variation in the size of seed crops in plants.**

is known as ***K*-selection**, or density-dependent selection. In contrast, selection for traits that maximize reproductive success in uncrowded environments (low densities) is called ***r*-selection**, or density-independent selection. These names follow from the variables of the logistic equation. *K*-selection is said to operate in populations living at a density near the limit imposed by their resources (the carrying capacity, *K*), where competition among individuals is stronger. Mature trees growing in an old-growth forest are an example of *K*-selected organisms. In contrast, *r*-selection is said to maximize *r*, the per capita rate of increase, and occurs in environments in which population densities are well below carrying capacity or individuals face little competition. Weeds growing in an abandoned agricultural field are an example of *r*-selected organisms.

Population Change and Population Density

Similar to the case of *r-selection*, a birth rate or death rate that does *not* change with population density is said to be **density independent**. In a classic study of population regulation, Andrew Watkinson and John Harper, of the University of Wales, found that the mortality of dune fescue grass (*Vulpia fasciculata*) is mainly due to physical factors that kill similar proportions of a local population, regardless of its density. For example, drought stress that arises when the roots of the grass are uncovered by shifting sands is a density-independent factor. In contrast, and similar to *K-selection*, a death rate that rises as population density rises is said to be **density dependent**, as is a birth rate that falls with rising density. Watkinson and Harper found that reproduction by dune fescue declines as population density increases, in part because water or nutrients become more scarce. Thus, the key factors regulating birth rate in this population are density dependent, while death rate is largely regulated by density-independent factors. **Figure 40.22** shows how the combination of density-dependent reproduction and density-independent mortality can stop population growth, leading to an equilibrium population density in species such as dune fescue.



▲ **Figure 40.22 Determining equilibrium for population density.** This simple model considers only birth and death rates. (Immigration and emigration rates are assumed to be either zero or equal.) In this example, the birth rate changes with population density, while the death rate is constant. At the equilibrium density (Q), the birth and death rates are equal.

DRAW IT *Redraw this figure for the case where the birth and death rates are both density dependent, as occurs for many species.*

Mechanisms of Density-Dependent Population Regulation

Without some type of negative feedback between population density and the rates of birth and death, a population would never stop growing. Density-dependent regulation provides that feedback, halting population growth through mechanisms that reduce birth rates or increase death rates. Several mechanisms of density-dependent population regulation are described in **Figure 40.23**.

These various examples of population regulation by negative feedback show how increased densities cause population growth rates to decline by affecting reproduction, growth, and survival. But while negative feedback helps explain why populations stop growing, it does not address why some populations fluctuate dramatically while others remain relatively stable. That is the topic we address next.

Population Dynamics

All populations for which we have long-term data show some fluctuation in size. Such population fluctuations from year to year or place to place, called **population dynamics**, are influenced by many factors and in turn affect other species, including our own. For example, fluctuations in fish populations influence seasonal harvests of commercially important species. The study of population dynamics focuses on the complex interactions between biotic and abiotic factors that cause variation in population sizes.

Stability and Fluctuation

Populations of large mammals were once thought to remain relatively stable over time, but long-term studies have challenged that idea. For instance, the moose population on Isle Royale in Lake Superior fluctuates substantially from year to year. What causes the size of this population to change so dramatically? Harsh weather, particularly cold winters, can weaken the moose and reduce food availability, decreasing the size of the population. When moose numbers are high, other factors, such as an increase in the density of ticks and other parasites, also cause the population to shrink.

Predation is an additional factor that regulates the population. Moose from the mainland colonized the island around 1900 by walking across the frozen lake. Wolves, which rely on moose for most of their food, followed around 1950. Because the lake has not frozen over in recent years, both populations have been isolated from immigration and emigration. Despite this isolation, the moose population experienced two major

▼ Figure 40.23 **Exploring Mechanisms of Density-Dependent Regulation**

As population density increases, many density-dependent mechanisms slow or stop population growth by decreasing birth rates or increasing death rates.

Competition for Resources

Increasing population density intensifies competition for nutrients and other resources, reducing reproductive rates. Farmers minimize the effect of resource competition on the growth of grains such as wheat (*Triticum aestivum*) and other crops by applying fertilizers to reduce nutrient limitations on crop yield.

Predation

Predation can be an important cause of density-dependent mortality if a predator captures more food as the population density of the prey increases. As a prey population builds up, predators may also feed preferentially on that species. Population increases in the collared lemming (*Dicrostonyx groenlandicus*) lead to density-dependent predation by several predators, including the snowy owl (*Bubo scandiacus*).

Disease

If the transmission rate of a disease increases as a population becomes more crowded, then the disease's impact is density dependent. In humans, the respiratory diseases influenza (flu) and tuberculosis are spread through the air when an infected person sneezes or coughs. Both diseases strike a greater percentage of people in densely populated cities than in rural areas.

Toxic Wastes

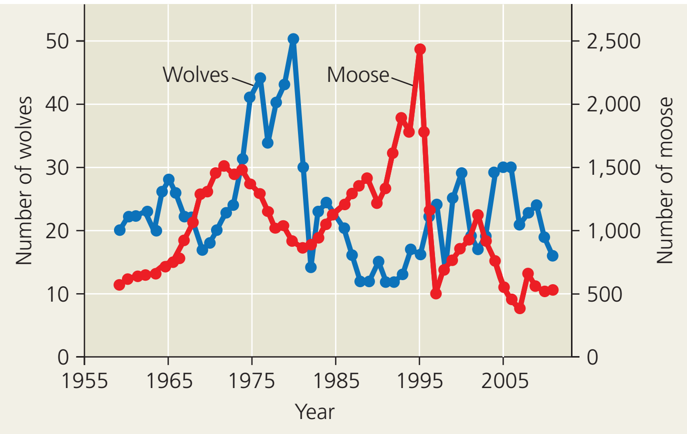
Yeasts, such as the brewer's yeast *Saccharomyces cerevisiae*, are used to convert carbohydrates to ethanol in winemaking. The ethanol that accumulates in the wine is toxic to yeasts and contributes to density-dependent regulation of yeast population size. The alcohol content of wine is usually less than 13% because that is the maximum concentration of ethanol that most wine-producing yeast cells can tolerate.

Territoriality

Territoriality can limit population density when space becomes the resource for which individuals compete. Cheetahs (*Acinonyx jubatus*) use a chemical marker in urine to warn other cheetahs of their territorial boundaries. The presence of surplus, or nonbreeding, individuals is a good indication that territoriality is restricting population growth.

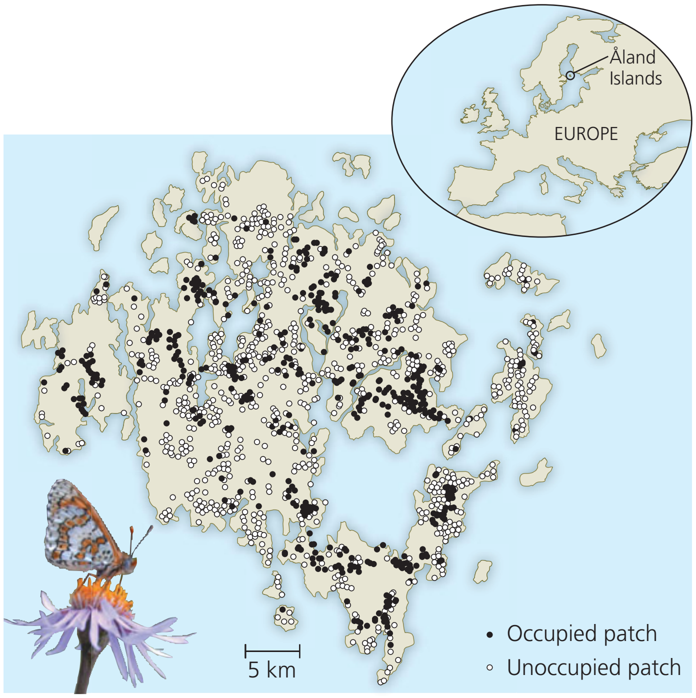
Intrinsic Factors

Intrinsic physiological factors sometimes regulate population size. Reproductive rates of white-footed mice (*Peromyscus leucopus*) in a field enclosure can drop even when food and shelter are abundant. This drop in reproduction at high population density is associated with aggressive interactions and hormonal changes that delay sexual maturation and depress the immune system.



▲ **Figure 40.24 Fluctuations in moose and wolf populations on Isle Royale, 1959–2011.**

BioFlix Visit the Study Area in **MasteringBiology** for the BioFlix® 3-D Animation on Population Ecology.



▲ **Figure 40.25 The Glanville fritillary: a metapopulation.** On the Åland Islands, local populations of this butterfly (filled circles) are found in only a fraction of the suitable habitat patches (open circles) at any given time. Individuals can move between local populations and colonize unoccupied patches.

increases and collapses during the last 50 years **(Figure 40.24)**. The first collapse coincided with a peak in the numbers of wolves from 1975 to 1980. The second collapse, around 1995, coincided with harsh winter weather, which increased the energy needs of the animals and made it harder for the moose to find food under the deep snow.

Immigration, Emigration, and Metapopulations

So far, our discussion of population dynamics has focused mainly on the contributions of births and deaths. However, immigration and emigration also influence populations. When a population becomes crowded and resource competition increases (see Figure 40.23), emigration often increases.

Immigration and emigration are particularly important when a number of local populations are linked, forming a **metapopulation**. Local populations in a metapopulation can be thought of as occupying discrete patches of suitable habitat in a sea of otherwise unsuitable habitat. Such patches vary in size, quality, and isolation from other patches, factors that influence how many individuals move among the populations. If one population becomes extinct, the patch it occupied can be recolonized by immigrants from another population.

The Glanville fritillary (*Melitaea cinxia*) illustrates the movement of individuals between populations. This butterfly is found in about 500 meadows across the Åland Islands of Finland, but its potential habitat in the islands is much larger, approximately 4,000 suitable patches. New populations of the butterfly regularly appear and existing populations become extinct, constantly shifting the locations of the 500 colonized patches **(Figure 40.25)**. The species persists in a balance of extinctions and recolonizations.

The metapopulation concept underscores the significance of immigration and emigration in the butterfly populations. It also helps ecologists understand population dynamics and gene flow in patchy habitats, providing a framework for the conservation of species living in a network of habitat fragments and reserves. In fact, many aspects of population ecology that you have studied in this chapter have practical applications. Farmers may want to reduce the abundance of insect pests or stop the growth of an invasive weed that is spreading rapidly. Conservation ecologists need to know what environmental factors create favorable feeding or breeding habitats for endangered species, such as the white rhinoceros and the whooping crane. Management programs based on population-regulating factors have helped prevent the extinction of many endangered species.

CONCEPT CHECK 40.6

1. In the fish called the peacock wrasse (*Symphodus tinca*), females disperse some of their eggs widely and lay other eggs in a nest. Only the latter receive parental care. Explain the trade-offs in reproduction that this behavior illustrates.
2. **WHAT IF?** Mice that experience stress such as a food shortage will sometimes abandon their young. Explain how this behavior might have evolved in the context of reproductive trade-offs and life history.
3. **MAKE CONNECTIONS** Negative feedback is a process that regulates biological systems (see Concept 32.1). Explain how the density-dependent birth rate of dune fescue grass exemplifies negative feedback.

For suggested answers, see Appendix A.

40 Chapter Review

SUMMARY OF KEY CONCEPTS

CONCEPT 40.1

Earth's climate influences the structure and distribution of terrestrial biomes (pp. 820–826)

- Global **climate** patterns are largely determined by the input of solar energy and Earth's revolution around the sun.
- The changing angle of the sun over the year, bodies of water, and mountains exert seasonal, regional, and local effects on **macroclimate**.
- **Climographs** show that temperature and precipitation are correlated with **biomes**. Other factors also influence biome location.
- Terrestrial biomes are often named for major physical or climatic factors and for their predominant vegetation. Vertical layering is an important feature of terrestrial biomes.

? *Some arctic tundra ecosystems receive as little rainfall as deserts but have much more dense vegetation. Based on Figure 40.8, what climatic factor might explain this difference?*

CONCEPT 40.2

Aquatic biomes are diverse and dynamic systems that cover most of Earth (pp. 827–830)

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

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

CONCEPT 40.3

Interactions between organisms and the environment limit the distribution of species (pp. 830–832)

- Ecologists want to know not only *where* species occur but also *why* those species occur where they do.
- The distribution of species may be limited by **dispersal**, **biotic** (living) factors, and **abiotic** (physical) factors, such as temperature extremes, salinity, and water availability.

? *If you were an ecologist studying the chemical and physical limits to the distributions of species, how might you rearrange the flowchart in Figure 40.12?*

CONCEPT 40.4

Dynamic biological processes influence population density, dispersion, and demographics (pp. 832–835)

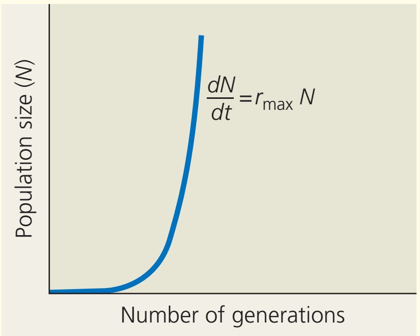
- Population **density**—the number of individuals per unit area or volume—reflects the interplay of births, deaths, immigration, and emigration. Environmental and social factors influence the **dispersion** of individuals.
- Populations increase from births and **immigration** and decrease from deaths and **emigration**. **Life tables**, **survivorship curves**, and **reproductive tables** summarize specific trends in **demography**.

? *Gray whales* (Eschrichtius robustus) *gather each winter near Baja California to give birth. How might such behavior make it easier for ecologists to estimate birth and death rates for the species?*

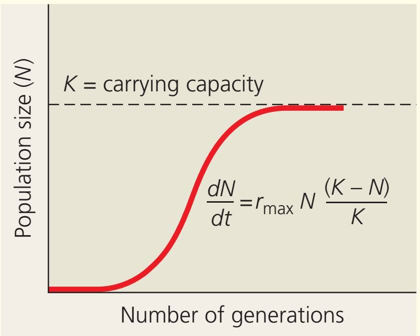
CONCEPT 40.5

The exponential and logistic models describe the growth of populations (pp. 835–839)

- If immigration and emigration are ignored, a population's growth rate (the per capita rate of increase) equals its birth rate minus its death rate.
- The **exponential growth** equation $dN/dt = r_{max}N$ represents a population's potential growth in an unlimited environment, where r_{max} is the maximum per capita rate of increase and N is the number of individuals in the population.



- Exponential growth cannot be sustained for long in any population. A more realistic population model limits growth by incorporating **carrying capacity** (K), the maximum population size the environment can support. According to the **logistic growth** equation $dN/dt = r_{max}N\,(K - N)/K$, growth levels off as population size approaches the carrying capacity.



- The logistic model fits few real populations perfectly, but it is useful for estimating possible growth.

? *As an ecologist who manages a wildlife preserve, you want to increase the preserve's carrying capacity for a particular endangered species. How might you go about accomplishing this?*

CONCEPT 40.6

Population dynamics are influenced strongly by life history traits and population density (pp. 839–842)

- **Life history** traits are evolutionary outcomes reflected in the development, physiology, and behavior of organisms.
- **Density-dependent** changes in birth and death rates curb population increase through negative feedback. Density-dependent limiting factors include intraspecific competition for limited food or space, increased predation, disease, intrinsic physiological factors, and buildup of toxic substances.

- All populations exhibit some size fluctuations, and many undergo regular boom-and-bust cycles influenced by complex interactions between biotic and abiotic factors. A **metapopulation** is a group of populations linked by immigration and emigration.

? *Name one biotic and one abiotic factor that contribute to yearly fluctuations in the size of the human population.*

TEST YOUR UNDERSTANDING

Level 1: Knowledge/Comprehension

1. Which of the following biomes is correctly paired with the description of its climate?
a. savanna—low temperature, precipitation uniform during the year
b. tundra—long summers, mild winters
c. temperate broadleaf forest—relatively short growing season, mild winters
d. temperate grasslands—relatively warm winters, most rainfall in summer
e. tropical forests—nearly constant day length and temperature

2. A population's carrying capacity
a. may change as environmental conditions change.
b. can be accurately calculated using the logistic growth model.
c. generally remains constant over time.
d. increases as the per capita growth rate (r) decreases.
e. can never be exceeded.

Level 2: Application/Analysis

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

4. According to the logistic growth equation

$$\frac{dN}{dt} = r_{max}N\frac{(K - N)}{K}$$

a. the number of individuals added per unit time is greatest when N is close to zero.
b. the per capita growth rate (r) increases as N approaches K.
c. population growth is zero when N equals K.
d. the population grows exponentially when K is small.
e. the birth rate (b) approaches zero as N approaches K.

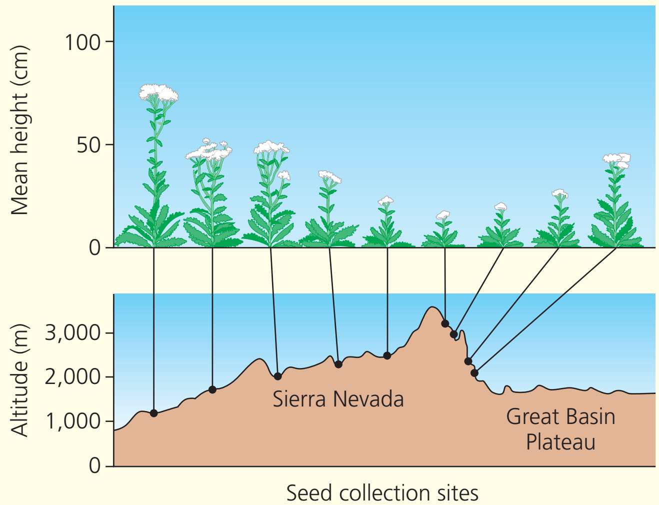
Level 3: Synthesis/Evaluation

5. **DRAW IT** After examining Figure 40.13, you decide to study feeding relationships among sea otters, sea urchins, and kelp. You know that sea otters prey on sea urchins and that urchins eat kelp. At four coastal sites, you measure kelp abundance. Then you spend one day at each site and mark whether otters are present or absent every 5 minutes during the day. Make a graph that shows how otter density depends on kelp abundance, using the data below. Then formulate a hypothesis to explain the pattern you observed.

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

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

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



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

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

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

9. **FOCUS ON INTERACTIONS**
In a short essay (100–150 words), identify the factor or factors in Figure 40.23 that you think may ultimately be most important for density-dependent population regulation in humans, and explain your reasoning.

For selected answers, see Appendix A.

41 Species Interactions

KEY CONCEPTS

41.1 Interactions within a community may help, harm, or have no effect on the species involved

41.2 Diversity and trophic structure characterize biological communities

41.3 Disturbance influences species diversity and composition

41.4 Biogeographic factors affect community diversity

41.5 Pathogens alter community structure locally and globally

OVERVIEW

Communities in Motion

Deep in the Lembeh Strait of Indonesia, a crab in the family Homolidae scuttles across the ocean floor holding a large sea urchin on its back **(Figure 41.1)**. When a predatory fish arrives, the crab settles quickly into the sediments and puts its living shield to use. The fish darts in and tries to bite the crab. In response, the crab tilts the spiny sea urchin toward whichever side the fish attacks. The fish eventually gives up and swims away.

The "carrier crab" in Figure 41.1 clearly benefits from having the sea urchin on its back. But how does the sea urchin fare in this relationship? Its association with the crab might harm it, help it, or have no effect on its survival and reproduction. For example, the sea urchin may be harmed if the crab sets it down in an unsuitable habitat or in a place where it is vulnerable to predators. On the other hand, the crab may also protect the sea urchin from predators while carrying it. Additional observations or experiments would be needed before ecologists could answer this question.

In Chapter 40, you learned how individuals within a population can affect other individuals of the same species. This chapter will examine ecological interactions between populations of different species. A group of populations of different species living close enough to interact is called a biological **community**. Ecologists define the boundaries of a particular community to fit their research questions: They might study the community of decomposers and other organisms living on a rotting log, the benthic community in Lake Superior, or the community of trees and shrubs in Great Smoky Mountains National Park in North Carolina and Tennessee.

We begin this chapter by exploring the kinds of interactions that occur between species in a community, such as the crab and sea urchin in Figure 41.1. We'll then consider several factors that are most significant in structuring a community—in determining how many species there are, which particular species are present, and the relative abundance of these species. Finally, we'll apply some of the principles of community ecology to the study of human disease.

▼ **Figure 41.1** Which species benefits from this interaction?

CONCEPT 41.1

Interactions within a community may help, harm, or have no effect on the species involved

Some key relationships in the life of an organism are its interactions with individuals of other species in the community. These **interspecific interactions** include competition, predation, herbivory, symbiosis (including parasitism, mutualism, and commensalism), and facilitation. In this section, we will define and describe each of these interactions, recognizing that ecologists do not always agree on the precise boundaries of each type of interaction.

We will use the symbols + and – to indicate how each interspecific interaction affects the survival and reproduction of the two species engaged in the interaction. For example, predation is a +/– interaction, with a positive effect on the survival and reproduction of the predator population and a negative effect on that of the prey population. Mutualism is a +/+ interaction because the survival and reproduction of both species are increased in the presence of the other. We use a 0 to indicate that a population is not affected by the interaction in any known way.

Competition

Interspecific competition is a –/– interaction that occurs when individuals of different species compete for a resource that limits their growth and survival. Weeds growing in a garden compete with garden plants for nutrients and water. Lynx and foxes in the northern forests of Alaska and Canada compete for prey such as snowshoe hares. In contrast, some resources, such as oxygen, are rarely in short supply, at least on land; most terrestrial species use this resource, but they do not usually compete for it.

Competitive Exclusion

What happens in a community when two species compete for limited resources? In 1934, Russian ecologist G. F. Gause studied this question using laboratory experiments with two species of ciliated protists, *Paramecium aurelia* and *Paramecium caudatum*. He cultured the species under stable conditions, adding a constant amount of food each day. When Gause grew the two species separately, each population grew rapidly and then leveled off at the apparent carrying capacity of the culture (see Figure 40.20a for an illustration of the logistic growth of *P. aurelia*). But when Gause grew the two species together, *P. caudatum* became extinct in the culture. Gause inferred that *P. aurelia* had a competitive edge in obtaining food. He concluded that two species competing for the same limiting resources cannot coexist permanently in the same place. In the absence of disturbance, one species will use the resources more efficiently and reproduce more rapidly than the other. Even a slight reproductive advantage will eventually lead to local elimination of the inferior competitor, an outcome called **competitive exclusion**.

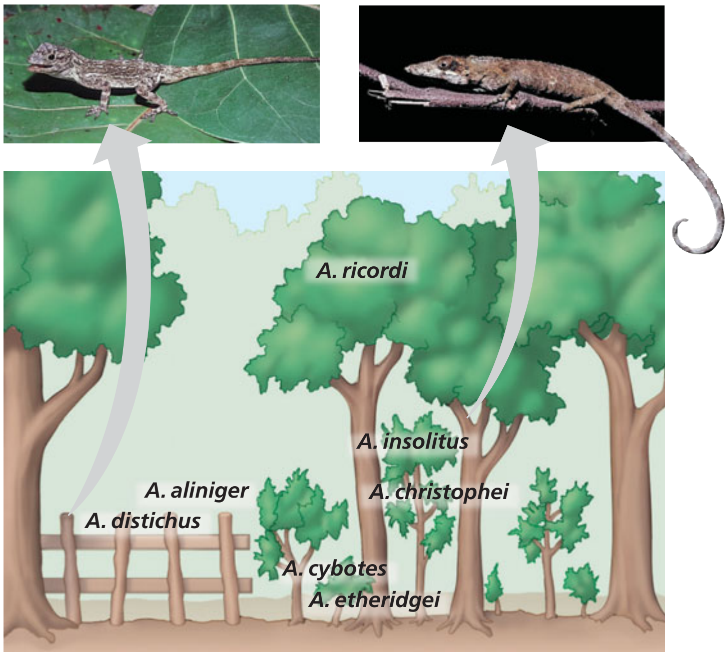
Ecological Niches and Natural Selection

EVOLUTION The influence of evolution is evident in the concept of the **ecological niche**, the specific set of biotic and abiotic resources that an organism uses in its environment. American ecologist Eugene Odum used the following analogy to explain the niche concept: If an organism's habitat is its "address," the niche is the organism's "profession." The niche of a tropical tree lizard, for instance, includes the temperature range it tolerates, the size of branches on which it perches, the time of day when it is active, and the sizes and kinds of insects it eats. Such factors define the lizard's niche, or ecological role—how it fits into an ecosystem.

We can use the niche concept to restate the principle of competitive exclusion: Two species cannot coexist permanently in a community if their niches are identical. However, ecologically similar species *can* coexist in a community if one or more significant differences in their niches arise through time. Evolution by natural selection can result in one of the species using a different set of resources or similar resources at different times of the day or year. The differentiation of niches that enables similar species to coexist in a community is called **resource partitioning** **(Figure 41.2)**. You can think of resource partitioning in a community as "the

A. distichus perches on fence posts and other sunny surfaces.

A. insolitus usually perches on shady branches.



▲ **Figure 41.2 Resource partitioning among Dominican Republic lizards.** Seven species of *Anolis* lizards live in close proximity, and all feed on insects and other small arthropods. However, competition for food is reduced because each lizard species has a different preferred perch, thus occupying a distinct niche.

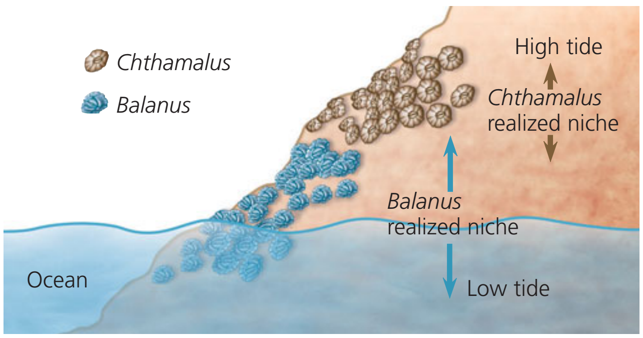
ghost of competition past"—the indirect evidence of earlier interspecific competition resolved by the evolution of niche differentiation.

As a result of competition, a species' *fundamental niche*, which is the niche potentially occupied by that species, is often different from its *realized niche*, the portion of its fundamental niche that it actually occupies in a particular environment. Ecologists can identify the fundamental niche of a species by testing the range of conditions in which it grows and reproduces in the absence of competitors. They can also test whether a potential competitor limits a species' realized niche by removing the competitor and seeing if the first species expands into the newly available space. The classic experiment depicted in **Figure 41.3** clearly showed that competition between two barnacle species kept one species from occupying part of its fundamental niche.

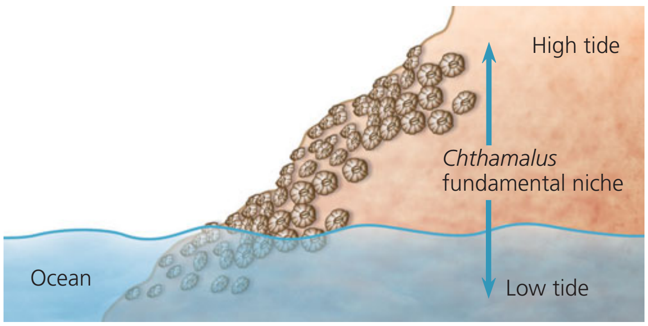
▼ Figure 41.3 Inquiry

Can a species' niche be influenced by interspecific competition?

Experiment Ecologist Joseph Connell studied two barnacle species—*Chthamalus stellatus* and *Balanus balanoides*—that have a stratified distribution on rocks along the coast of Scotland. *Chthamalus* is usually found higher on the rocks than *Balanus*. To determine whether the distribution of *Chthamalus* is the result of interspecific competition with *Balanus*, Connell removed *Balanus* from the rocks at several sites.



Results *Chthamalus* spread into the region formerly occupied by *Balanus*.



Conclusion Interspecific competition makes the realized niche of *Chthamalus* much smaller than its fundamental niche.

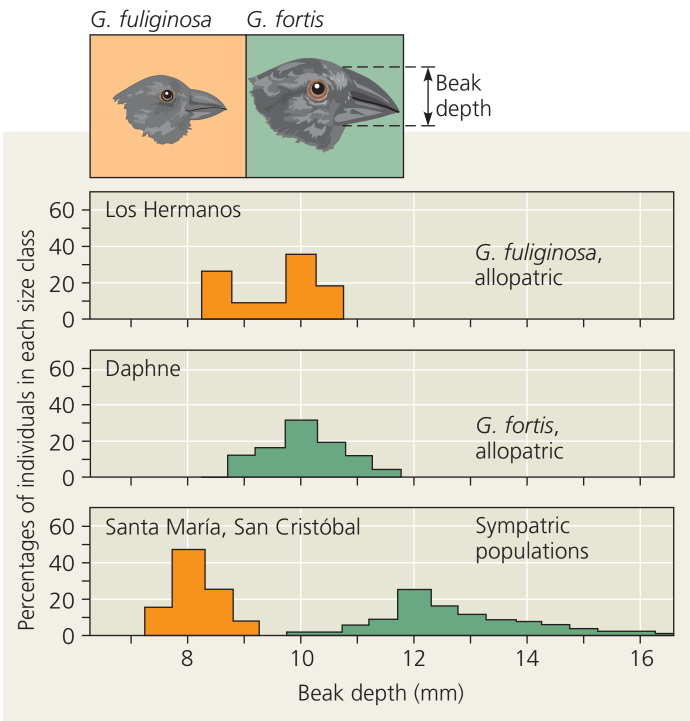
Source J. H. Connell, The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*, *Ecology* 42:710–723 (1961).

MB See the related Experimental Inquiry Tutorial in MasteringBiology.

WHAT IF? Other observations showed that *Balanus* cannot survive high on the rocks because it dries out during low tides. How would *Balanus*'s realized niche compare with its fundamental niche?

Character Displacement

Closely related species whose populations are sometimes allopatric (geographically separate; see Chapter 22) and sometimes sympatric (geographically overlapping) provide more evidence for the importance of competition in structuring communities. In some cases, the allopatric populations of such species are morphologically similar and use similar resources. By contrast, sympatric populations, which would potentially compete for resources, show differences in body structures and in the resources they use. This tendency for characteristics to diverge more in sympatric than in allopatric populations of two species is called **character displacement**. An example of character displacement in Galápagos finches is shown in **Figure 41.4**.



▲ Figure 41.4 Character displacement: indirect evidence of past competition. Allopatric populations of *Geospiza fuliginosa* and *Geospiza fortis* on Los Hermanos and Daphne Islands have similar beak morphologies (top two graphs) and presumably eat similarly sized seeds. However, where the two species are sympatric on Santa María and San Cristóbal, *G. fuliginosa* has a shallower, smaller beak and *G. fortis* a deeper, larger one (bottom graph), adaptations that favor eating different-sized seeds.

? *If the beak length of* G. fortis *is typically 12% longer than the beak depth, what is the predicted beak length of* G. fortis *individuals with the smallest beak depths observed on Santa María and San Cristóbal Islands?*

Predation

Predation refers to a +/– interaction between species in which one species, the predator, kills and eats the other, the prey. Though the term *predation* generally elicits such images as a lion attacking and eating an antelope, it applies to a wide range of interactions. An animal that kills a plant by eating the plant's tissues can also be considered a predator. Because eating and avoiding being eaten are prerequisite to reproductive success, the adaptations of both predators and prey tend to be refined through natural selection (see Concept 27.5). In the **Scientific Skills Exercise**, you can interpret data from an experiment investigating a specific predator-prey interaction.

Many important feeding adaptations of predators are obvious and familiar. Most predators have acute senses that enable them to find and identify potential prey. Rattlesnakes and other pit vipers, for example, find their prey with a pair of heat-sensing organs located between their eyes and nostrils (see Figure 38.17a). Many predators also have adaptations such as claws, teeth, stingers, or poison that help them catch and subdue their food. Predators that pursue their prey are generally fast and agile, whereas those that lie in ambush are often disguised in their environments.

Just as predators possess adaptations for capturing prey, potential prey animals have adaptations that help them avoid being eaten. Some common behavioral defenses are hiding, fleeing, and forming herds or schools. Active self-defense is less common, though some large grazing mammals vigorously defend their young from predators such as lions.

Animals also display a variety of morphological and physiological defensive adaptations. **Cryptic coloration**, or camouflage, makes prey difficult to see **(Figure 41.5a)**. Mechanical or chemical defenses protect species such as porcupines and skunks. Some animals, including the European fire salamander, can synthesize toxins, whereas others accumulate toxins passively from the plants they eat. Animals with effective chemical defenses often exhibit bright **aposematic coloration**, or warning coloration, such as that of the poison dart frog **(Figure 41.5b)**. Such coloration seems to be adaptive because predators often avoid brightly colored prey.

Some prey species are protected by their resemblance to other species. In **Batesian mimicry**, a palatable or harmless species mimics an unpalatable or harmful one. The larva of the hawkmoth *Hemeroplanes ornatus* puffs up its head and thorax when disturbed, looking like the head of a small venomous snake **(Figure 41.5c)**. In this case, the mimicry even involves behavior; the larva weaves its head back and forth and hisses like a snake. In **Müllerian mimicry**, two or more unpalatable species, such as the cuckoo bee and yellow jacket, resemble each other **(Figure 41.5d)**. In an example of convergent evolution, unpalatable animals in several different taxa have similar patterns of coloration: Black and yellow or red stripes characterize unpalatable animals as diverse as yellow jackets and coral snakes.

Many predators also use mimicry. The alligator snapping turtle has a tongue that resembles a wriggling worm, which is used to lure small fish. Any fish that tries to eat the "bait" is itself quickly consumed as the turtle's strong jaws snap closed.

▼ **Figure 41.5 Examples of defensive coloration in animals.**

(a) Cryptic coloration

▶ Canyon tree frog

(b) Aposematic coloration

▶ Poison dart frog

(c) Batesian mimicry: A harmless species mimics a harmful one.

◀ Nonvenomous hawkmoth larva

▼ Venomous green parrot snake

(d) Müllerian mimicry: Two unpalatable species mimic each other.

◀ Cuckoo bee

▼ Yellow jacket

Herbivory

Ecologists use the term **herbivory** to refer to a +/− interaction in which an organism eats parts of a plant or alga. While large mammalian herbivores such as cattle, sheep, and water buffalo may be most familiar, most herbivores are actually invertebrates, such as grasshoppers, caterpillars, and beetles. In the ocean, herbivores include sea urchins, some tropical fishes, and certain mammals, including the manatee **(Figure 41.6)**.

Like predators, herbivores have many specialized adaptations. Many herbivorous insects have chemical sensors on their feet that enable them to distinguish between toxic and nontoxic plants or between more nutritious and less nutritious plants. Some mammalian herbivores, such as goats, use their sense of smell to examine plants. They may also eat just a specific part of a plant, such as the flowers. Many herbivores also have specialized teeth or digestive systems adapted to processing vegetation (see Chapter 33).

Unlike prey animals, plants cannot run away to avoid being eaten. Instead, a plant's arsenal against herbivores may feature chemical toxins or structures such as spines and thorns. Among the plant compounds that serve as chemical weapons are the poison strychnine, produced by the tropical vine *Strychnos toxifera*, and nicotine, from the tobacco plant. Compounds that are not toxic to humans but may be distasteful to many herbivores are responsible for the familiar flavors of cinnamon, cloves, and peppermint.

▲ **Figure 41.6 A marine herbivore.** This West Indian manatee (*Trichechus manatus*) in Florida is grazing on *Hydrilla*, an introduced plant.

Symbiosis

When individuals of two or more species live in direct and intimate contact with one another, their relationship is called **symbiosis**. In this text, we define symbiosis to include all such

Scientific Skills Exercise

Using Bar Graphs and Scatter Plots to Present and Interpret Data

Can a Native Predator Species Adapt Rapidly to an Introduced Prey Species? Cane toads (*Bufo marinus*) were introduced to Australia in 1935 in a failed attempt to control an insect pest. Since then, the toads have spread throughout northeastern Australia, reaching a population of over 200 million today. Cane toads have glands that produce a toxin that is poisonous to snakes and other potential predators of the toads. In this exercise, you will graph and interpret data from a two-part experiment conducted to determine whether native Australian predators have developed resistance to the cane toad toxin.

How the Experiment Was Done In part 1, researchers collected 12 black snakes (*Pseudechis porphyriacus*) from areas where cane toads had existed for 40–60 years and another 12 from areas free of cane toads. They offered the snakes either a freshly killed native frog (*Limnodynastes peronii*, a species the snakes commonly eat) or a freshly killed cane toad from which the toxin gland had been removed (making the toad nonpoisonous). In part 2, researchers collected snakes from areas where cane toads had been present for 5–60 years. To assess how cane toad toxin affected these snakes, they injected small amounts of the toxin into the snakes' stomachs and measured the snakes' swimming speed in a small pool.

Data from the Experiment, Part 1

Type of Prey Offered	Percentage of Snakes That Ate Prey Offered in Each Area: Cane Toads Present in Area for 40–60 Years	Percentage of Snakes That Ate Prey Offered in Each Area: No Cane Toads in Area
Native frog	100	100
Cane toad	0	50

Data from the Experiment, Part 2

Time Since First Exposure to Cane Toads (years)	5	10	10	20	50	60	60	60	60	60
Percentage Reduction in Swimming Speed	52	19	30	30	5	5	9	11	12	22

Interpret the Data

1. Make a bar graph of the data in part 1. (For additional information about graphs, see the Scientific Skills Review in Appendix F and in the Study Area in MasteringBiology.)
2. What do the data represented in the graph suggest about the effects of cane toads on the predatory behavior of black snakes in areas where the toads are and are not currently found?
3. Suppose an enzyme that deactivates the cane toad toxin evolves in black snakes living in areas with cane toads. If the researchers repeated part 1 of this study, predict how the results would change.
4. Identify the dependent and independent variables in part 2. Make a scatter plot of the data.
5. Based on the scatter plot, what conclusion would you draw about whether exposure to cane toads is having a selective effect on black snakes in this study? Explain.
6. Explain why a bar graph is an appropriate type of graph for presenting the data in part 1 and a scatter plot is an appropriate type for presenting the data in part 2.

Data from B. L. Phillips and R. Shine, An invasive species induces rapid adaptive change in a native predator: cane toads and black snakes in Australia, *Proceedings of the Royal Society B* 273:1545–1550 (2006).

MB A version of this Scientific Skills Exercise can be assigned in MasteringBiology.

interactions, whether they are harmful, helpful, or neutral. Some biologists define symbiosis more narrowly as a synonym for mutualism, an interaction in which both species benefit.

Parasitism

Parasitism is a +/– symbiotic interaction in which one organism, the **parasite**, derives its nourishment from another organism, its **host**, which is harmed in the process. Parasites that live within the body of their host, such as tapeworms, are called **endoparasites**; parasites that feed on the external surface of a host, such as ticks and lice, are called **ectoparasites**. In one particular type of parasitism, parasitoid insects—usually small wasps—lay eggs on or in living hosts. The larvae then feed on the body of the host, eventually killing it. Some ecologists have estimated that at least one-third of all species on Earth today are parasites.

Many parasites have complex life cycles involving multiple hosts. The blood fluke, which infects approximately 200 million people around the world, requires two hosts for its development: humans and freshwater snails. Some parasites change the behavior of their current host in ways that increase the likelihood that the parasite will reach its next host. For instance, crustaceans that are parasitized by acanthocephalan (spiny-headed) worms leave protective cover and move into the open, where they are more likely to be eaten by the birds that are the second host in the worm's life cycle.

Parasites can significantly affect the survival, reproduction, and density of their host population, either directly or indirectly. For example, ticks that live as ectoparasites on moose weaken their hosts by withdrawing blood and causing hair breakage and loss. In their weakened condition, the moose have a greater chance of dying from cold stress or predation by wolves (see Figure 40.24).

Mutualism

Mutualistic symbiosis, or **mutualism**, is an interspecific interaction that benefits both species (+/+). You have seen examples of mutualism in previous chapters: Examples of mutualism include nitrogen fixation by bacteria in the root nodules of legumes; cellulose digestion by microorganisms in the digestive systems of termites and ruminant mammals; and photosynthesis by unicellular algae in corals. In the acacia-ant example shown in **Figure 41.7**, both species can survive alone. In some other cases, though, such as termites and microorganisms, both species have lost the ability to survive on their own.

Mutualism typically involves the coevolution of related adaptations in both species, with changes in either species likely to affect the survival and reproduction of the other. For example, most flowering plants have adaptations such as nectar or fruit that attract animals that pollinate flowers or disperse seeds (see Chapter 30). In turn, many animals have adaptations that help them find and consume nectar.

(a) Certain species of acacia trees in Central and South America have hollow thorns that house stinging ants of the genus *Pseudomyrmex*. The ants feed on nectar produced by the tree and on protein-rich swellings along the bases of the leaves.

(b) The acacia benefits because the pugnacious ants, which attack anything that touches the tree, remove fungal spores, small herbivores, and debris. They also clip vegetation that grows close to the acacia.

▲ Figure 41.7 Mutualism between acacia trees and ants.

Commensalism

An interaction between species that benefits one of the species but neither harms nor helps the other (+/0) is called **commensalism**. Commensal interactions are difficult to document in nature because any close association between species likely affects both species, even if only slightly. For instance, "hitchhiking" species, such as algae that live on the shells of aquatic turtles or barnacles that attach to whales, are sometimes considered commensal. The hitchhikers gain a place to grow while having seemingly little effect on their ride. However, they may reduce the hosts' efficiency of movement in searching for food or escaping from predators. Conversely, the hitchhikers may help camouflage the hosts.

Some commensal associations involve one species obtaining food that is inadvertently exposed by another. Cattle egrets feed on insects flushed out of the grass by grazing bison, cattle,

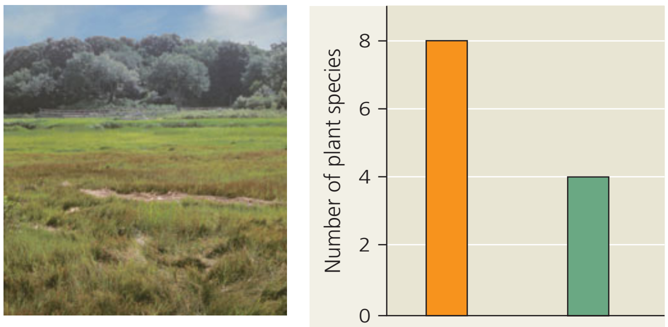
▲ **Figure 41.8 A possible example of commensalism between cattle egrets and African buffalo.**

and other herbivores **(Figure 41.8)**. Because the birds typically find more prey when they follow herbivores, they clearly benefit from the association. Much of the time, the herbivores may be unaffected by the birds. However, they, too, may derive some benefit; the birds occasionally remove and eat ticks and other ectoparasites from the herbivores or may warn the herbivores of a predator's approach.

Facilitation

Species can have positive effects (+/+ or 0/+) on the survival and reproduction of other species without necessarily living in the direct and intimate contact of a symbiosis. This type of interaction, called **facilitation**, is particularly common in plant ecology. For instance, the black rush *Juncus gerardii* makes the soil more hospitable for other plant species in some zones of New England salt marshes **(Figure 41.9a)**. *Juncus* helps prevent salt buildup in the soil by shading the soil surface, which reduces evaporation. *Juncus* also prevents the salt marsh soils from becoming oxygen depleted as it transports oxygen to its belowground tissues. In one study, when *Juncus* was removed from areas in the upper middle intertidal zone, those areas supported 50% fewer plant species **(Figure 41.9b)**.

All five types of interactions discussed so far—competition, predation, herbivory, symbiosis, and facilitation—strongly influence the structure of communities. You'll see other examples of these interactions throughout this chapter.



(a) Salt marsh with *Juncus* (foreground)

(b)

▲ **Figure 41.9 Facilitation by black rush (*Juncus gerardii*) in New England salt marshes.** Black rush increases the number of plant species that can live in the upper middle zone of the marsh.

CONCEPT CHECK 41.1

1. Explain how interspecific competition, predation, and mutualism differ in their effects on the interacting populations of two species.
2. According to the principle of competitive exclusion, what outcome is expected when two species with identical niches compete for a resource? Why?
3. **MAKE CONNECTIONS** Figure 22.12 illustrates the formation of and possible outcomes for a hybrid zone over time. Imagine that two finch species colonize a new island and are capable of hybridizing (mating and producing viable offspring). The island contains two plant species, one with large seeds and one with small seeds, growing in isolated habitats. If the two finch species specialize in eating different plant species, would reproductive barriers be reinforced, weakened, or unchanged in this hybrid zone? Explain.

For suggested answers, see Appendix A.

CONCEPT 41.2

Diversity and trophic structure characterize biological communities

Along with the specific interactions described in the previous section, communities are also characterized by more general attributes, including how diverse they are and the feeding relationships of their species. In this section, you'll see why such ecological attributes are important. You'll also learn how a few species sometimes exert strong control on a community's structure, particularly on the composition, relative abundance, and diversity of its species.

Species Diversity

The **species diversity** of a community—the variety of different kinds of organisms that make up the community—has two components. One is **species richness**, the number of different species in the community. The other is the **relative abundance** of the different species, the proportion each species represents of all individuals in the community.

Imagine two small forest communities, each with 100 individuals distributed among four tree species (A, B, C, and D) as follows:

Community 1: 25A, 25B, 25C, 25D

Community 2: 80A, 5B, 5C, 10D

The species richness is the same for both communities because they both contain four species of trees, but the relative abundance is very different **(Figure 41.10)**. You would easily notice the four types of trees in community 1, but without looking carefully, you might see only the abundant species A in the second forest. Most observers would intuitively describe community 1 as the more diverse of the two communities.

Ecologists use many tools to compare the diversity of communities across time and space. They often calculate indexes of diversity based on species richness and relative abundance. One widely used index is the **Shannon diversity index** (H):

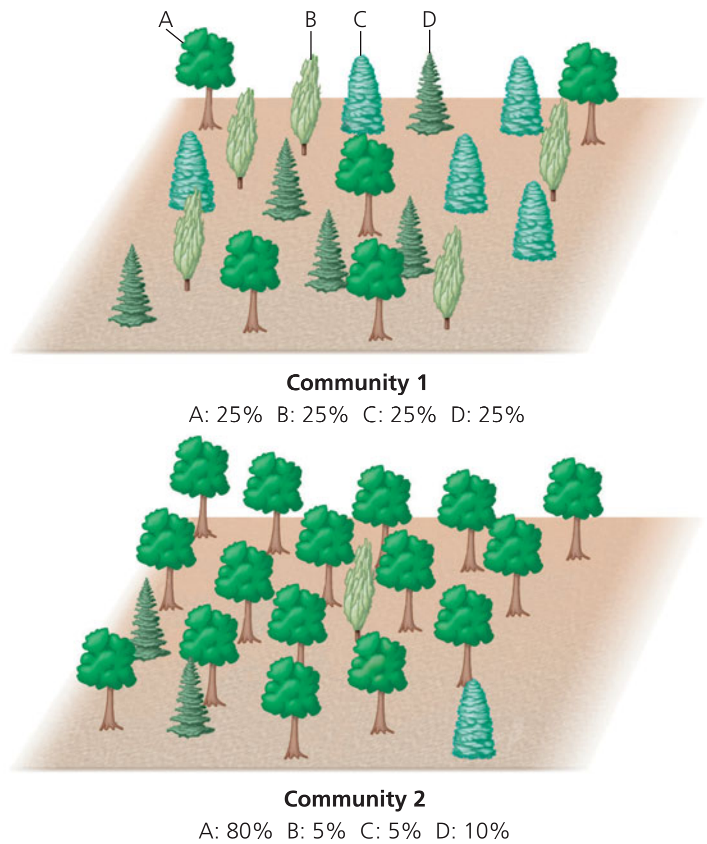
$$H = -(p_A \ln p_A + p_B \ln p_B + p_C \ln p_C + \ldots)$$

where A, B, C . . . are the species in the community, p is the relative abundance of each species, and ln is the natural logarithm. A higher value of H indicates a more diverse community. Let's use this equation to calculate the Shannon diversity index of the two communities in Figure 41.10. For community 1, $p = 0.25$ for each species, so

$$H = -4(0.25 \ln 0.25) = 1.39$$

For community 2,

$$H = -[0.8 \ln 0.8 + 2(0.05 \ln 0.05) + 0.1 \ln 0.1] = 0.71$$



▲ **Figure 41.10 Which forest is more diverse?** Ecologists would say that community 1 has greater species diversity, a measure that includes both species richness and relative abundance.

These calculations confirm that community 1 is more diverse.

Determining the number and relative abundance of species in a community can be challenging. Because most species in a community are relatively rare, it may be hard to obtain a sample size large enough to be representative. It is also difficult to census highly mobile or less visible organisms, such as insects and nocturnal species. The small size of microorganisms makes them particularly difficult to sample, so ecologists now use molecular tools to help determine microbial diversity **(Figure 41.11)**.

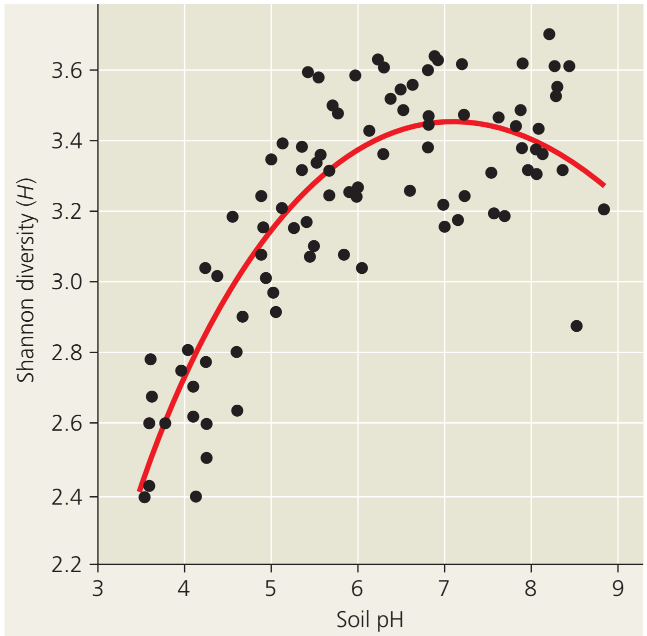
▼ **Figure 41.11 Research Method**

Determining Microbial Diversity Using Molecular Tools

Application Ecologists are increasingly using molecular techniques, such as the analysis of restriction fragment length polymorphisms (RFLPs), to determine microbial diversity and richness in environmental samples. Noah Fierer and Rob Jackson, of Duke University, used RFLP analysis to compare the diversity of soil bacteria in 98 habitats across North and South America to help identify environmental variables associated with high bacterial diversity.

Technique Researchers first extract and purify DNA from the microbial community in each sample. They use the polymerase chain reaction (see Chapter 13) to amplify specific DNA (such as that encoding small ribosomal subunit RNA) and label the DNA with a fluorescent dye. Restriction enzymes then cut the amplified, labeled DNA into fragments of different lengths, which are separated by gel electrophoresis. The number and abundance of these fragments characterize the DNA profile of the sample. Based on their RFLP analysis, Fierer and Jackson calculated the Shannon diversity index (H) of each sample. They then looked for a correlation between H and several environmental variables.

Results The diversity of the sampled bacteria was related almost exclusively to soil pH, with the Shannon diversity index being highest in neutral soils and lowest in acidic soils.



Source N. Fierer and R. B. Jackson, The diversity and biogeography of soil bacterial communities, *Proceedings of the National Academy of Sciences USA* 103:626–631 (2006).

▲ **Figure 41.12 Study plots at the Cedar Creek Natural History Area, site of long-term experiments in which researchers have manipulated plant diversity.**

Diversity and Community Stability

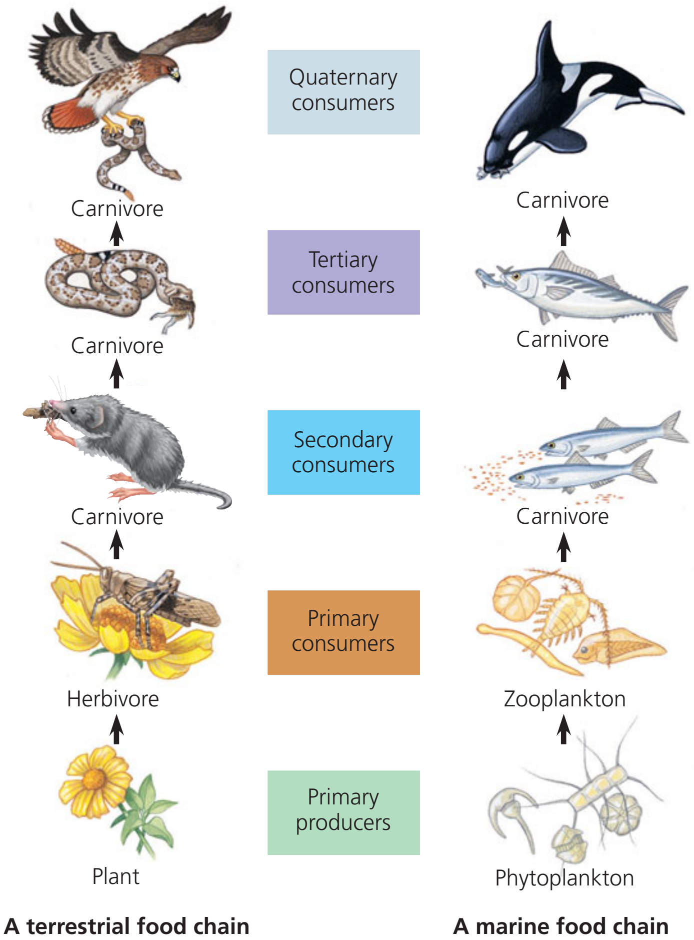
In addition to measuring species diversity, ecologists manipulate diversity in experimental communities in nature and in the laboratory. They do this to examine the potential benefits of diversity, including increased productivity and stability of biological communities.

Researchers at the Cedar Creek Natural History Area, in Minnesota, have been manipulating plant diversity in experimental communities for two decades **(Figure 41.12)**. Higher-diversity communities generally are more productive and are better able to withstand and recover from environmental stresses, such as droughts. More diverse communities are also more stable year to year in their productivity. In one decade-long experiment, for instance, researchers at Cedar Creek created 168 plots, each containing 1, 2, 4, 8, or 16 perennial grassland species. The most diverse plots produced **biomass** (the total mass of all individuals in a population) much more consistently than the single-species plots each year.

Higher-diversity communities are often more resistant to **invasive species**, which are organisms that become established outside their native range. Scientists working in Long Island Sound, off the coast of Connecticut, created communities with different levels of diversity consisting of sessile marine invertebrates, including tunicates (see Concept 27.3). They then examined how vulnerable these experimental communities were to invasion by an exotic tunicate. They found that the exotic tunicate was four times more likely to survive in lower-diversity communities than in higher-diversity ones. The researchers concluded that relatively diverse communities captured more of the resources available in the system, leaving fewer resources for the invader and decreasing its survival.

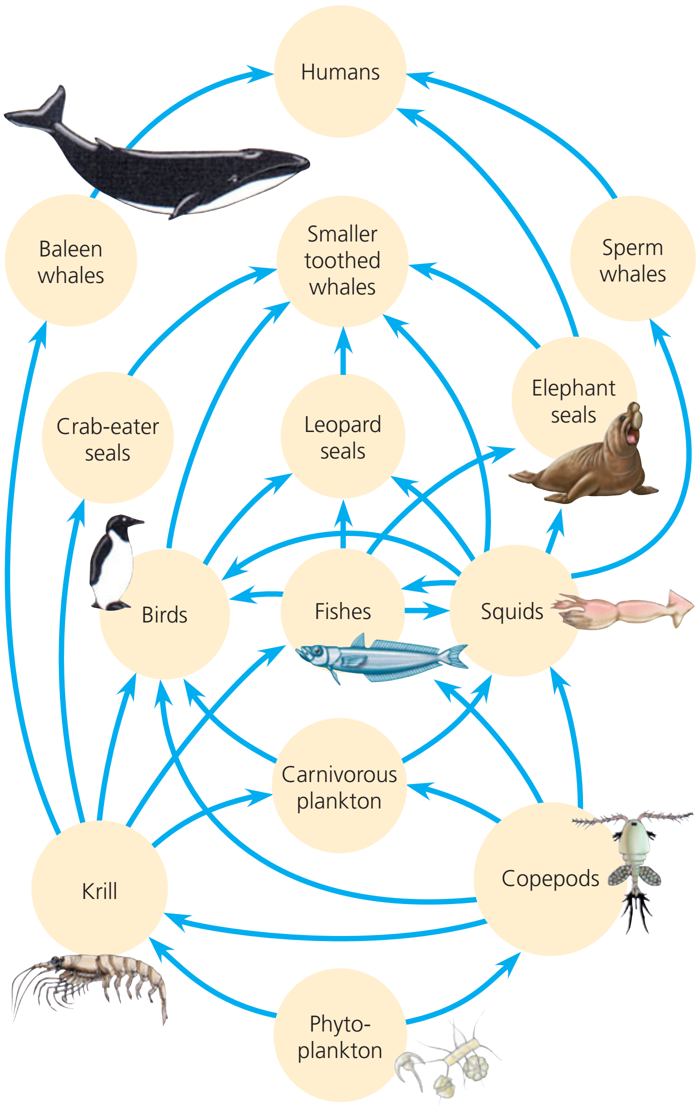
Trophic Structure

Experiments like the ones just described often examine the importance of diversity within one trophic level. The structure and dynamics of a community also depend on the feeding relationships between organisms in different trophic levels. These relationships together make up the **trophic structure** of the community. The transfer of food energy up the trophic levels from its source in plants and other autotrophs (primary producers) through herbivores (primary consumers) to carnivores (secondary, tertiary, and quaternary consumers) and eventually to decomposers is referred to as a **food chain (Figure 41.13)**.



▲ **Figure 41.13 Examples of terrestrial and marine food chains.** The arrows trace energy and nutrients that pass through the trophic levels of a community when organisms feed on one another. Decomposers, which "feed" on organisms from all trophic levels, are not shown here.

In the 1920s, Oxford University biologist Charles Elton recognized that food chains are not isolated units but are linked together in **food webs**. Ecologists diagram the trophic relationships of a community using arrows linking species according to who eats whom. In an Antarctic pelagic community, for example, the primary producers are phytoplankton, which serve as food for the dominant grazing zooplankton, especially krill and copepods, both of which are crustaceans. These zooplankton species are in turn eaten by carnivores, including other plankton, penguins, seals, fishes, and baleen whales. Squids, which are carnivores that feed on fish and zooplankton, are another



▲ **Figure 41.14 An Antarctic marine food web.** Arrows follow the transfer of food from the producers (phytoplankton) up through the trophic levels. For simplicity, this diagram omits decomposers.

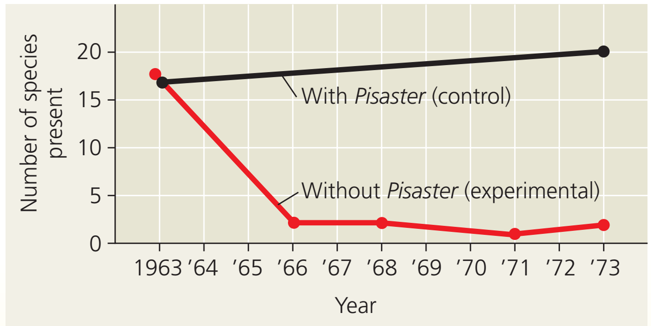
▼ **Figure 41.15 Inquiry**

Is *Pisaster ochraceus* a keystone predator?

Experiment In rocky intertidal communities of western North America, the relatively uncommon sea star *Pisaster ochraceus* preys on mussels such as *Mytilus californianus*, a dominant species and strong competitor for space.

Robert Paine, of the University of Washington, removed *Pisaster* from an area in the intertidal zone and examined the effect on species richness.

Results In the absence of *Pisaster*, species richness declined as mussels monopolized the rock face and eliminated most other invertebrates and algae. In a control area where *Pisaster* was not removed, species richness changed very little.



Conclusion *Pisaster* acts as a keystone species, exerting an influence on the community that is not reflected in its abundance.

Source R. T. Paine, Food web complexity and species diversity, *American Naturalist* 100:65–75 (1966).

WHAT IF? Suppose that an invasive fungus killed most individuals of *Mytilus* at these sites. Predict how species richness would be affected if *Pisaster* were then removed.

important link in these food webs, as they are in turn eaten by seals and toothed whales (**Figure 41.14**).

Note that a given species may weave into the web at more than one trophic level. In the food web shown in Figure 41.14, krill feed on phytoplankton as well as on other grazing zooplankton, such as copepods.

Species with a Large Impact

Certain species have an especially large impact on the structure of entire communities because they are highly abundant or play a pivotal role in community dynamics. The impact of these species occurs through trophic interactions and their influence on the physical environment.

Dominant species in a community are the species that are the most abundant or that collectively have the highest biomass. There is no single explanation for why a species becomes dominant in a community. One hypothesis suggests that dominant species are competitively superior in exploiting limited resources such as water or nutrients. Another hypothesis is that dominant species are most successful at avoiding predation or the impact of disease. This latter idea could explain the high biomass attained by some invasive species. Such species may not face the natural predators or parasites that would otherwise hold their populations in check.

In contrast to dominant species, **keystone species** are not usually abundant in a community. They exert strong control on community structure not by numerical might but by their pivotal ecological roles, or niches. **Figure 41.15** highlights the importance of a keystone species, a sea star, in maintaining the diversity of an intertidal community.

Other organisms exert their influence on a community not through trophic interactions but by changing their physical

▲ **Figure 41.16 Beavers as ecosystem engineers.** By felling trees, building dams, and creating ponds, beavers can transform large areas of forest into flooded wetlands.

environment. Species that dramatically alter their environment are called **ecosystem engineers** or, to avoid implying conscious intent, "foundation species." A familiar ecosystem engineer is the beaver **(Figure 41.16)**. The effects of ecosystem engineers on other species can be positive or negative, depending on the needs of the other species.

Bottom-Up and Top-Down Controls

Simplified models based on relationships between adjacent trophic levels are useful for describing community organization. For example, consider the three possible relationships between plants (V for vegetation) and herbivores (H):

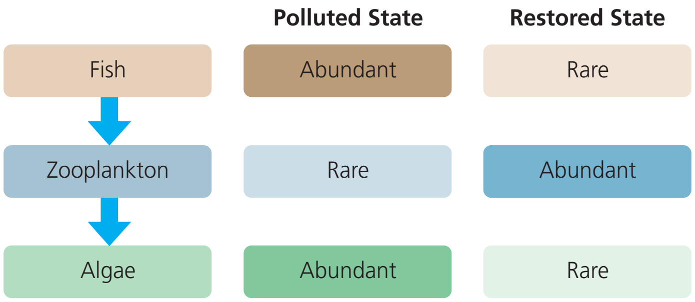
$$V \rightarrow H \qquad V \leftarrow H \qquad V \leftrightarrow H$$

The arrows indicate that a change in the biomass of one trophic level causes a change in the other trophic level. $V \rightarrow H$ means that an increase in vegetation will increase the numbers or biomass of herbivores, but not vice versa. In this situation, herbivores are limited by vegetation, but vegetation is not limited by herbivory. In contrast, $V \leftarrow H$ means that an increase in herbivore biomass will decrease the abundance of vegetation, but not vice versa. A double-headed arrow indicates that each trophic level is sensitive to changes in the biomass of the other.

Two models of community organization are common: the bottom-up model and the top-down model. The $V \rightarrow H$ linkage suggests a **bottom-up model**, which postulates a unidirectional influence from lower to higher trophic levels. In this case, the presence or absence of mineral nutrients (N) controls plant (V) numbers, which control herbivore (H) numbers, which in turn control predator (P) numbers. The simplified bottom-up model is thus $N \rightarrow V \rightarrow H \rightarrow P$. To change the community structure of a bottom-up community, you need to alter biomass at the lower trophic levels, allowing those changes to propagate up through the food web. If you add mineral nutrients to stimulate plant growth, then the higher trophic levels should also increase in biomass. If you change predator abundance, however, the effect should not extend down to the lower trophic levels.

In contrast, the **top-down model** postulates the opposite: Predation mainly controls community organization because predators limit herbivores, herbivores limit plants, and plants limit nutrient levels through nutrient uptake. The simplified top-down model, $N \leftarrow V \leftarrow H \leftarrow P$, is also called the *trophic cascade model*. In a lake community with four trophic levels, the model predicts that removing the top carnivores will increase the abundance of primary carnivores, in turn decreasing the number of herbivores, increasing phytoplankton abundance, and decreasing concentrations of mineral nutrients. The effects thus move down the trophic structure as alternating +/− effects.

Ecologists have applied the top-down model to improve water quality in polluted lakes. This approach, called **biomanipulation**, attempts to prevent algal blooms and eutrophication by altering the density of higher-level consumers instead of using chemical treatments. In lakes with three trophic levels, removing fish should improve water quality by increasing zooplankton density, thereby decreasing algal populations. In lakes with four trophic levels, adding top predators should have the same effect. We can summarize the scenario of three trophic levels with the following diagram:



Ecologists in Finland used biomanipulation to help purify Lake Vesijärvi, a large lake that was polluted with city sewage and industrial wastewater until 1976. After pollution controls reduced these inputs, the water quality of the lake began to improve. By 1986, however, massive blooms of cyanobacteria started to occur in the lake. These blooms coincided with an increase in the population of roach, a fish species that eats zooplankton, which otherwise keep the cyanobacteria and algae in check. To reverse these changes, ecologists removed nearly a million kilograms of fish between 1989 and 1993, reducing roach abundance by about 80%. At the same time, they added a fourth trophic level by stocking the lake with pike perch, a predatory fish that eats roach. The water became clear, and the last cyanobacterial bloom was in 1989. The lake remains clear even though roach removal ended in 1993.

As these examples show, communities vary in their degree of bottom-up and top-down control. To manage agricultural landscapes, parks, reservoirs, and fisheries, we need to understand each particular community's dynamics.

CONCEPT CHECK 41.2

1. What two components contribute to species diversity? Explain how two communities with the same number of species can differ in species diversity.
2. Based on the food web in Figure 41.14, identify all of the organisms that eat and are eaten by elephant seals.
3. **WHAT IF?** Consider a grassland with five trophic levels: grasses, mice, snakes, raccoons, and bobcats. If you released additional bobcats into the grassland, how would plant biomass change if the bottom-up model applied? If the top-down model applied? Explain.

For suggested answers, see Appendix A.

CONCEPT 41.3

Disturbance influences species diversity and composition

Decades ago, most ecologists favored the traditional view that biological communities are at equilibrium, a more or less stable balance, unless seriously disturbed by human activities. The "balance of nature" view focused on interspecific competition as a key factor determining community composition and maintaining stability in communities. *Stability* in this context refers to a community's tendency to reach and maintain a relatively constant composition of species.

One of the earliest proponents of this view, F. E. Clements, of the Carnegie Institution of Washington, argued in the early 1900s that the community of plants at a site had only one stable equilibrium, a *climax community* controlled solely by climate. According to Clements, biotic interactions caused the species in this climax community to function as an integrated unit. His argument was based on the observation that certain species of plants are consistently found together, such as the oaks, maples, birches, and beeches in deciduous forests of the northeastern United States.

Other ecologists questioned whether most communities were at equilibrium or functioned as integrated units. A. G. Tansley, of Oxford University, challenged the concept of a climax community, arguing that differences in soils, topography, and other factors created many potential communities that were stable within a region. H. A. Gleason, of the University of Chicago, saw communities more as chance assemblages of species with similar abiotic requirements—for example, for temperature, rainfall, and soil type. Gleason and other ecologists also realized that disturbance keeps many communities from reaching a stable state in species diversity or composition. A **disturbance** is an event, such as a storm, fire, drought, or human activity, that changes a community by removing organisms from it or altering resource availability.

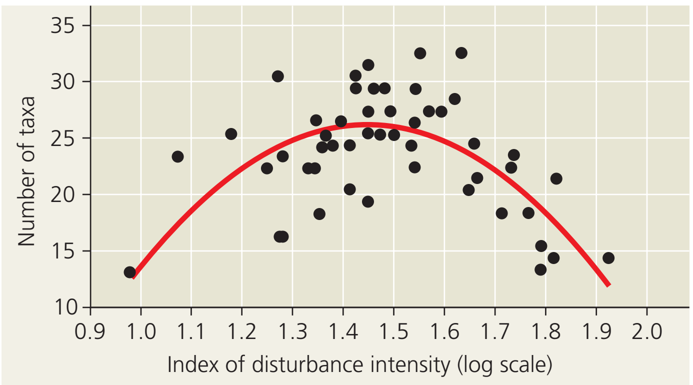
This recent emphasis on change has produced the **nonequilibrium model**, which describes most communities as constantly changing after disturbance. Even relatively stable communities can be rapidly transformed into nonequilibrium communities. Let's examine some of the ways disturbance influences community structure and composition.

Characterizing Disturbance

The types of disturbances and their frequency and severity vary among communities. Storms disturb most communities, even many in the oceans through the action of waves. Fire is a significant disturbance; in fact, chaparral and some grassland biomes require regular burning to maintain their structure and species composition. Many streams and ponds are disturbed by spring flooding and seasonal drying. A high level of disturbance is generally the result of frequent *and* intense disturbance, while low disturbance levels can result from either a low frequency or low intensity of disturbance.

The **intermediate disturbance hypothesis** states that moderate levels of disturbance foster greater species diversity than do low or high levels of disturbance. High levels of disturbance reduce diversity by creating environmental stresses that exceed the tolerances of many species or by disturbing the community so often that slow-growing or slow-colonizing species are excluded. At the other extreme, low levels of disturbance can reduce species diversity by allowing competitively dominant species to exclude less competitive ones. Meanwhile, intermediate levels of disturbance can foster greater species diversity by opening up habitats for occupation by less competitive species. Such intermediate disturbance levels rarely create conditions so severe that they exceed the environmental tolerances or recovery rates of potential community members.

The intermediate disturbance hypothesis is supported by many terrestrial and aquatic studies. In one study, ecologists in New Zealand compared the richness of invertebrate taxa living in the beds of streams exposed to different frequencies and intensities of flooding **(Figure 41.17)**. When floods occurred



▲ **Figure 41.17 Testing the intermediate disturbance hypothesis.** Researchers identified the taxa (species or genera) of invertebrates at two locations in each of 27 New Zealand streams. They assessed the intensity of flooding at each location using an index of streambed disturbance. The number of invertebrate taxa peaked where the intensity of flooding was at intermediate levels.

either very frequently or rarely, invertebrate richness was low. Frequent floods made it difficult for some species to become established in the streambed, while rare floods resulted in species being displaced by superior competitors. Invertebrate richness peaked in streams that had an intermediate frequency or intensity of flooding, as predicted by the hypothesis.

Although moderate levels of disturbance appear to maximize species diversity, small and large disturbances often have important effects on community structure. Small-scale disturbances can create patches of different habitats across a landscape, which help maintain diversity in a community. Large-scale disturbances are also a natural part of many communities. Much of Yellowstone National Park, for example, is dominated by lodgepole pine, a tree species that requires the rejuvenating influence of periodic fires. Lodgepole pinecones remain closed until exposed to intense heat. When a forest fire burns the trees, the cones open and the seeds are released. The new generation of lodgepole pines can then thrive on nutrients released from the burned trees and in the sunlight that is no longer blocked by taller trees.

In the summer of 1988, extensive areas of Yellowstone burned during a severe drought. By 1989, burned areas in the park were largely covered with new vegetation, suggesting that the species in this community are adapted to rapid recovery after fire **(Figure 41.18)**. In fact, large-scale fires have periodically swept through the lodgepole pine forests of Yellowstone and other northern areas for thousands of years.

Studies of the Yellowstone forest community and many others indicate that they are nonequilibrium communities, changing continually because of natural disturbances and the internal processes of growth and reproduction. Mounting evidence suggests that nonequilibrium conditions are in fact the norm for most communities.

Ecological Succession

Changes in the composition and structure of terrestrial communities are most apparent after some severe disturbance, such as a volcanic eruption or a glacier, strips away all the existing vegetation. The disturbed area may be colonized by a variety of species, which are gradually replaced by other species, which are in turn replaced by still other species—a process called **ecological succession**. When this process begins in a virtually lifeless area where soil has not yet formed, such as on a new volcanic island or on the rubble (moraine) left by a retreating glacier, it is called **primary succession**. In contrast, **secondary succession** occurs when an existing community has been cleared by some disturbance that leaves the soil intact, as in Yellowstone following the 1988 fires (see Figure 41.18).

During primary succession, the only life-forms initially present are often prokaryotes and protists. Lichens and mosses, which grow from windblown spores, are commonly the first macroscopic photosynthesizers to colonize such areas. Soil develops gradually as rocks weather and organic matter accumulates from the decomposed remains of the early colonizers. Once soil is present, the lichens and mosses are usually overgrown by grasses, shrubs, and trees that sprout from seeds blown in or carried in by animals. Eventually, an area is colonized by plants that become the community's dominant vegetation. Producing such a community through primary succession may take hundreds or thousands of years.

Early-arriving species and later-arriving ones are often linked by one of three processes. The early arrivals may *facilitate* the appearance of the later species by making the environment more favorable—for example, by increasing the fertility of the soil. Alternatively, the early species may *inhibit* establishment of the later species, so that successful colonization occurs in spite of, rather than because of, the activities of the early species.

(a) Soon after fire. The fire has left a patchy landscape. Note the unburned trees in the far distance.

(b) One year after fire. The community has begun to recover. Herbaceous plants, different from those in the former forest, cover the ground.

▲ **Figure 41.18 Recovery following a large-scale disturbance.** The 1988 Yellowstone National Park fires burned large areas of forests dominated by lodgepole pines.

Finally, the early species may be completely independent of the later species, which *tolerate* conditions created early in succession but are neither helped nor hindered by early species.

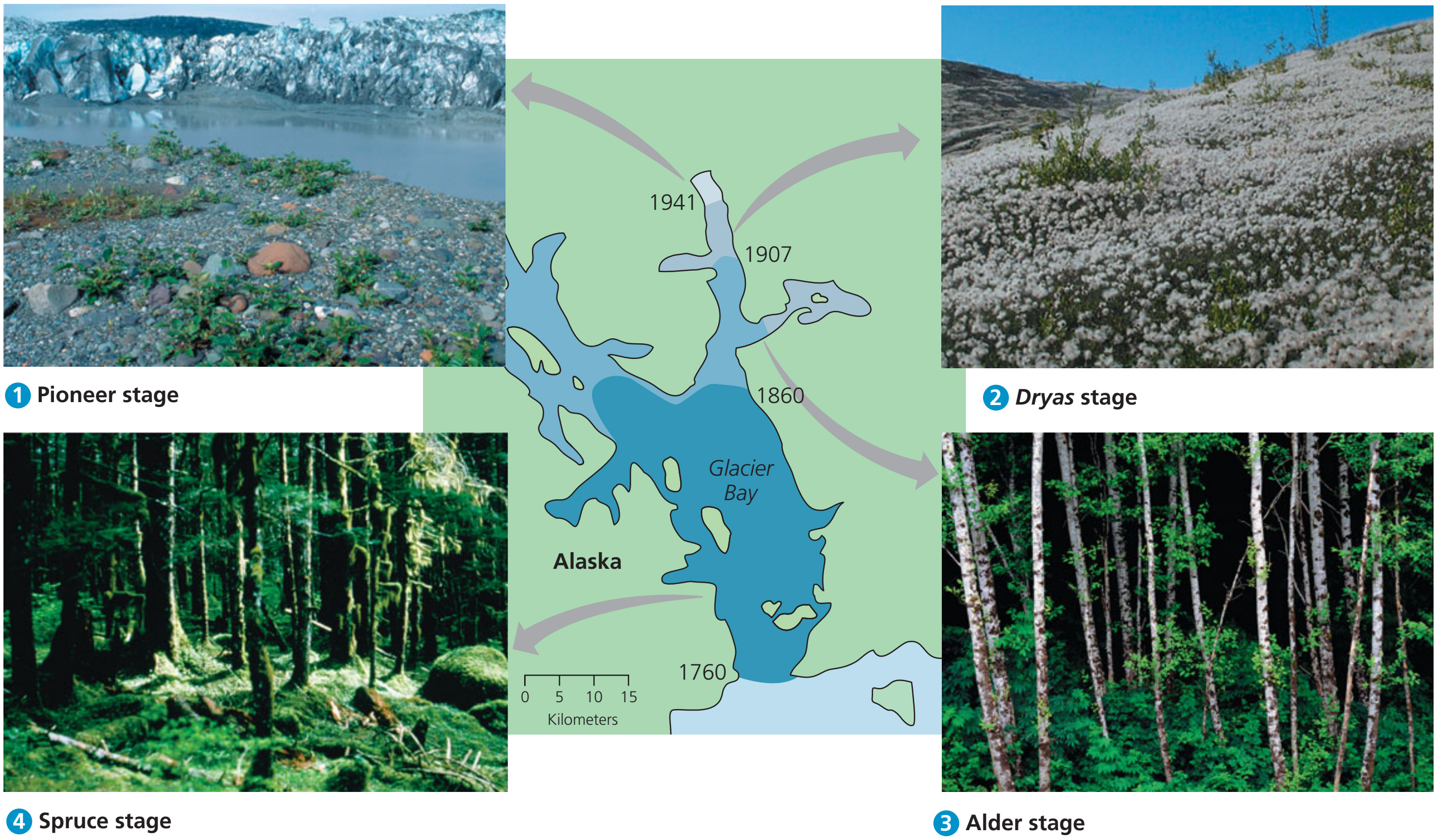
Ecologists have conducted some of the most extensive research on primary succession at Glacier Bay in southeastern Alaska, where glaciers have retreated more than 100 km since 1760 **(Figure 41.19)**. By studying the communities on moraines at different distances from the mouth of the bay, ecologists can examine different stages in succession. ❶ The exposed moraine is colonized first by pioneering species that include liverworts, mosses, fireweed, scattered *Dryas* (a mat-forming shrub), and willows. ❷ After about three decades, *Dryas* dominates the plant community. ❸ A few decades later, the area is invaded by alder, which forms dense thickets up to 9 m tall. ❹ In the next two centuries, these alder stands are overgrown first by Sitka spruce and later by a combination of western hemlock and mountain hemlock. In areas of poor drainage, the forest floor of this spruce-hemlock forest is invaded by sphagnum moss, which holds water and acidifies the soil, eventually killing the trees. Thus, by about 300 years after glacial retreat, the vegetation consists of sphagnum bogs on the poorly drained flat areas and spruce-hemlock forest on the well-drained slopes.

Succession on glacial moraines is related to environmental changes in soil nutrients and other environmental factors caused by transitions in the vegetation. Because the bare soil after glacial retreat is low in nitrogen, almost all the pioneer plants begin succession with poor growth and yellow leaves due to nitrogen deficiency. The exceptions are *Dryas* and alder, which have symbiotic bacteria that fix atmospheric nitrogen (see Chapter 29). Soil nitrogen increases quickly during the alder stage of succession and keeps increasing during the spruce stage. By altering soil properties, pioneer plant species can facilitate colonization by new plant species during succession.

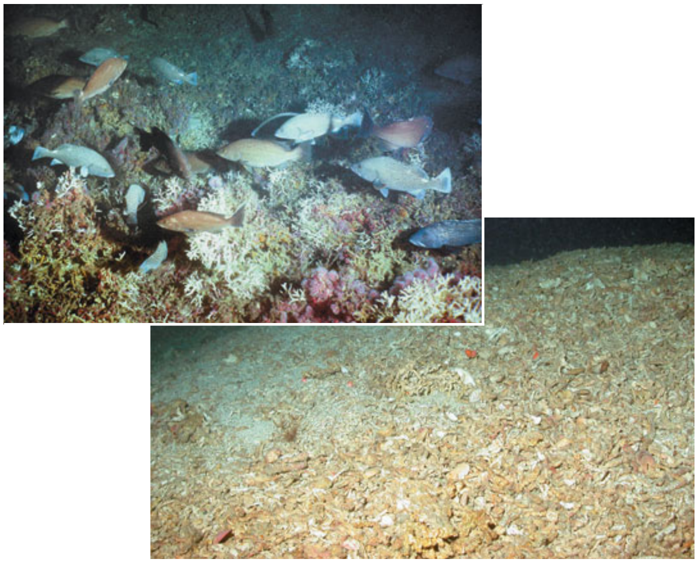
Human Disturbance

Ecological succession is a response to disturbance of the environment, and the strongest agent of disturbance today is human activity. Agricultural development has disrupted what were once the vast grasslands of the North American prairie. Tropical rain forests are quickly disappearing as a result of clear-cutting for lumber, cattle grazing, and farmland. Centuries of overgrazing and agricultural disturbance have contributed to famine in parts of Africa by turning seasonal grasslands into vast barren areas.

Humans disturb marine ecosystems as well as terrestrial ones. The effects of ocean trawling, where boats drag weighted nets across the seafloor, are similar to those of clear-cutting a forest or plowing a field **(Figure 41.20)**. The trawls scrape and scour corals and other life on the seafloor. In a typical year, ships trawl an area about the size of South America, 150 times larger than the area of forests that are clear-cut annually.



▲ **Figure 41.19 Glacial retreat and primary succession at Glacier Bay, Alaska.** The different shades of blue on the map show retreat of the glacier since 1760, based on historical descriptions.



▲ **Figure 41.20 Disturbance of the ocean floor by trawling.** These photos show the seafloor off northwestern Australia before (top) and after (bottom) deep-sea trawlers have passed.

Because disturbance by human activities is often severe, it reduces species diversity in many communities. In Chapter 43, we'll take a closer look at how human-caused disturbance is affecting the diversity of life.

CONCEPT CHECK 41.3

1. Why do high and low levels of disturbance usually reduce species diversity? Why does an intermediate level of disturbance promote species diversity?
2. During succession, how might the early species facilitate the arrival of other species?
3. **WHAT IF?** Most prairies experience regular fires, typically every few years. These disturbances tend to be relatively modest. How would the species diversity of a prairie likely be affected if no burning occurred for 100 years? Explain your answer.

For suggested answers, see Appendix A.

CONCEPT 41.4

Biogeographic factors affect community diversity

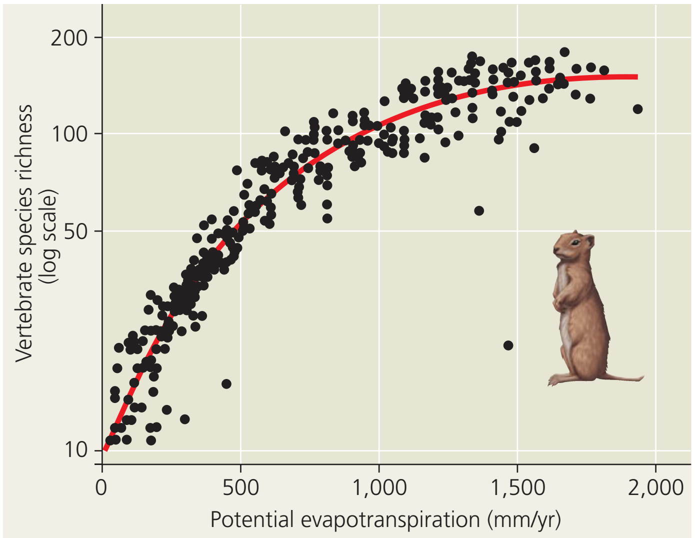
So far, we have examined relatively small-scale or local factors that influence the diversity of communities, including the effects of species interactions, dominant species, and many types of disturbances. Ecologists also recognize that large-scale biogeographic factors contribute to the range of diversity observed in communities. The contributions of two biogeographic factors in particular—the latitude of a community and the area it occupies—have been investigated for more than a century.

Latitudinal Gradients

In the 1850s, both Charles Darwin and Alfred Wallace pointed out that plant and animal life was generally more abundant and diverse in the tropics than in other parts of the globe. Since that time, many researchers have confirmed this observation. One study found that a 6.6-hectare plot (1 ha = 10,000 m^2) in tropical Malaysia contained 711 tree species, while a 2-ha plot of deciduous forest in Michigan typically contained just 10 to 15 tree species. Many groups of animals show similar latitudinal gradients.

The two key factors affecting latitudinal gradients of species richness are probably evolutionary history and climate. Over the course of evolutionary time, species richness may increase in a community as more speciation events occur (see Chapter 22). Tropical communities are generally older than temperate or polar communities, which have repeatedly "started over" after major disturbances from glaciations. Also, the growing season in tropical forests is about five times as long as in the tundra communities of high latitudes. In effect, biological time runs about five times as fast in the tropics as near the poles, so intervals between speciation events are shorter in the tropics.

Climate is a primary cause of the latitudinal gradient in richness and diversity. In terrestrial communities, the two main climatic factors correlated with diversity are sunlight and precipitation, both of which are relatively abundant in the tropics. These factors can be considered together by measuring a community's rate of **evapotranspiration**, the evaporation of water from soil and plants together. Evapotranspiration, a function of solar radiation, temperature, and water availability, is much higher in hot areas with abundant rainfall than in areas with low temperatures or low precipitation. *Potential evapotranspiration*, a measure of potential water loss that assumes that water is readily available, is determined by the amount of solar radiation and temperature and is highest in regions where both are plentiful. The species richness of animals as well as plants correlates well with both measures, as shown for vertebrates and potential evapotranspiration in **Figure 41.21**.



▲ **Figure 41.21 Energy, water, and species richness.** Vertebrate species richness in North America increases most predictably with potential evapotranspiration, expressed as rainfall equivalents (mm/yr).

Area Effects

In 1807, naturalist and explorer Alexander von Humboldt described one of the first patterns of species richness to be recognized, the **species-area curve**: All other factors being equal, the larger the geographic area of a community, the more species it has, in part because larger areas offer a greater diversity of habitats and microhabitats. The basic concept of diversity increasing with increasing area applies in many situations, from surveys of ant diversity in New Guinea to studies of plant species richness on islands of different sizes.

Because of their isolation and limited size, islands provide excellent opportunities for studying the biogeographic factors that affect the species diversity of communities. By "islands," we mean not only oceanic islands, but also habitat islands on land, such as lakes, mountain peaks, and habitat fragments—any patch surrounded by an environment not suitable for the "island" species. American ecologists Robert MacArthur and E. O. Wilson developed a general model of island biogeography, identifying the key determinants of species diversity on an island with a given set of physical characteristics.

Consider a newly formed oceanic island that receives colonizing species from a distant mainland. Two factors that determine the number of species on the island are the rate at which new species immigrate to the island and the rate at which species become extinct on the island. At any given time, an island's immigration and extinction rates are affected by the number of species already present. As the number of species on the island increases, the immigration rate of new species decreases, because any individual reaching the island is less likely to represent a species that is not already present. At the same time, as more species inhabit an island, extinction rates on the island increase because of the greater likelihood of competitive exclusion.

Two physical features of the island further affect immigration and extinction rates: its size and its distance from the mainland. Small islands generally have lower immigration rates because potential colonizers are less likely to reach a small island than a large one. Small islands also have higher extinction rates because they generally contain fewer resources, have less diverse habitats, and have smaller populations. Distance from the mainland is also important; a closer island generally has a higher immigration rate and lower extinction rate than one farther away. Arriving colonists help sustain the presence of a species on a near island and prevent its extinction.

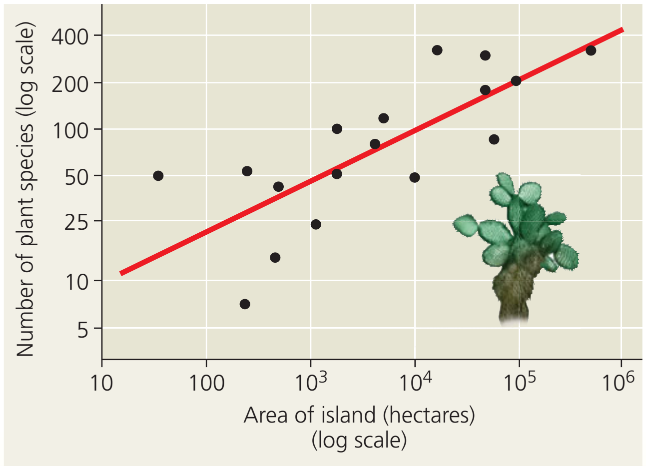
MacArthur and Wilson's model is called the *island equilibrium model* because an equilibrium will eventually be reached where the rate of species immigration equals the rate of species extinction. The number of species at this equilibrium point is correlated with the island's size and distance from the mainland. Like any ecological equilibrium, this species equilibrium is dynamic; immigration and extinction continue, and the exact species composition may change over time.

▼ **Figure 41.22 Inquiry**

How does species richness relate to area?

Field Study Ecologists Robert MacArthur and E. O. Wilson studied the number of plant species on the Galápagos Islands in relation to the area of the different islands.

Results



Conclusion Plant species richness increases with island size, supporting the island equilibrium model.

Source R. H. MacArthur and E. O. Wilson, *The Theory of Island Biogeography*, Princeton University Press, Princeton, NJ (1967).

WHAT IF? Four islands in this study ranging in area from about 40 to 10,000 ha each contained about 50 plant species. What does such variation tell you about the simple assumptions of the island equilibrium model?

MacArthur and Wilson's studies of the diversity of plants and animals on island chains support the prediction that species richness increases with island size, in keeping with the island equilibrium model **(Figure 41.22)**. Species counts also fit the prediction that the number of species decreases with increasing remoteness of the island.

Over long periods, disturbances such as storms, adaptive evolutionary changes, and speciation generally alter the species composition and community structure on islands. Nonetheless, the island equilibrium model is widely applied in ecology. Conservation biologists in particular use it when designing habitat reserves or establishing a starting point for predicting the effects of habitat loss on species diversity.

CONCEPT CHECK 41.4

1. Describe two hypotheses that explain why species diversity is greater in tropical regions than in temperate and polar regions.
2. Describe how an island's size and distance from the mainland affect the island's species richness.
3. **WHAT IF?** Based on MacArthur and Wilson's island equilibrium model, how would you expect the richness of birds on islands to compare with the richness of snakes and lizards?

For suggested answers, see Appendix A.

CONCEPT 41.5

Pathogens alter community structure locally and globally

Now that we have examined several important factors that structure biological communities, we will finish the chapter by examining community interactions involving **pathogens**—disease-causing organisms and viruses. Scientists have only recently come to appreciate how universal the effects of pathogens are in structuring ecological communities.

Effects on Community Structure

Pathogens produce especially clear effects on community structure when they are introduced into new habitats. Coral reef communities, for example, are increasingly susceptible to the influence of newly discovered pathogens. White-band disease, caused by an unknown pathogen, has resulted in dramatic changes in the structure and composition of Caribbean reefs. The disease kills corals by causing their tissue to slough off in a band from the base to the tip of the branches. Because of the disease, staghorn coral (*Acropora cervicornis*) has virtually disappeared from the Caribbean since the 1980s. Populations of elkhorn coral (*Acropora palmata*) have also been decimated. Such corals provide key habitat for lobsters as well as snappers and other fish species. When the corals die, they are quickly overgrown by algae. Surgeonfish and other herbivores that feed on algae come to dominate the fish community. Eventually, the corals topple because of damage from storms and other disturbances. The complex, three-dimensional structure of the reef disappears, and diversity plummets.

Pathogens also influence community structure in terrestrial ecosystems. In the forests and savannas of California, trees of several species are dying from sudden oak death (SOD). This recently discovered disease is caused by the fungus-like protist *Phytophthora ramorum* (see Chapter 25). SOD was first described in California in 1995, when hikers noticed trees dying around San Francisco Bay. By 2011, it had spread more than 1,000 km. During that time, it killed more than a million oaks and other trees from the central California coast to southern Oregon. The loss of these oaks has led to the decreased abundance of at least five bird species, including the acorn woodpecker and the oak titmouse, that rely on the oaks for food and habitat. Although there is currently no cure for SOD, scientists recently sequenced the genome of *P. ramorum* in hopes of finding a way to fight the pathogen.

Community Ecology and Zoonotic Diseases

Three-quarters of emerging human diseases and many of the most devastating diseases are caused by **zoonotic pathogens**—those that are transferred to humans from other animals, either through direct contact with an infected animal or by means of an intermediate species, called a **vector**. The vectors that spread zoonotic diseases are often parasites, including ticks, lice, and mosquitoes.

Identifying the community of hosts and vectors for a pathogen can help prevent diseases such as Lyme disease, which is spread by ticks. For years, scientists thought that the primary host for the Lyme pathogen was the white-footed mouse because mice are heavily parasitized by young ticks **(Figure 41.23)**. When researchers vaccinated mice against Lyme disease and released them into the wild, however, the number of infected ticks hardly changed. Further investigation in New York revealed that two inconspicuous shrew species were the hosts of more than half the ticks collected in the field. Identifying the dominant hosts for a pathogen provides information that may be used to control the hosts most responsible for spreading diseases.

Ecologists also use their knowledge of community interactions to track the spread of zoonotic diseases. For example, avian flu is caused by highly contagious viruses transmitted through the saliva and feces of birds (see Chapter 17). Most of these viruses affect wild birds mildly, but they often cause stronger symptoms in domesticated birds, the most common source of human infections. Since 2003, one particular viral strain, called H5N1, has killed hundreds of millions of poultry and more than 300 people. Millions more people are at risk of infection.

Control programs that quarantine domestic birds or monitor their transport may be ineffective if avian flu spreads naturally through the movements of wild birds. From 2003 to 2006, the H5N1 strain spread rapidly from southeast Asia into Europe and Africa, but by early 2012, it had not appeared in Australia or the Americas. The most likely place for infected wild birds to enter the Americas is Alaska, the entry point for ducks, geese, and shorebirds that migrate every year across the Bering Sea from Asia. Ecologists are studying the spread of the

▲ **Figure 41.23 Identifying Lyme disease host species.** A student researcher collects ticks from a white-footed mouse. Genetic analysis of the ticks from a variety of hosts enabled scientists to identify the former hosts of other ticks collected in the field that were no longer attached to a host.

▲ **Figure 41.24 Tracking avian flu.** Graduate student Travis Booms, of Boise State University, bands a young gyrfalcon as part of a project to monitor the spread of the disease.

virus by trapping and testing migrating and resident birds in Alaska **(Figure 41.24)**.

Human activities are transporting pathogens around the world at unprecedented rates. Genetic analyses suggest that *P. ramorum* likely came to North America from Europe in nursery plants. Similarly, the pathogens that cause human diseases are spread by our global economy. H1N1, the virus that causes "swine flu" in humans, was first detected in Veracruz, Mexico, in early 2009. It quickly spread around the world when infected individuals flew on airplanes to other countries. By the time the outbreak ended in 2010, the first flu pandemic in 40 years had killed more than 17,000 people.

Community ecology provides the foundation for understanding the life cycles of pathogens and their interactions with hosts. Pathogen interactions are also greatly influenced by changes in the physical environment. To control pathogens and the diseases they cause, scientists need an ecosystem perspective—an intimate knowledge of how the pathogens interact with other species and with all aspects of their environment. Ecosystems are the subject of Chapter 42.

CONCEPT CHECK 41.5

1. What are pathogens?
2. **WHAT IF?** Rabies, a viral disease in mammals, is not currently found in the British Isles. If you were in charge of disease control there, what practical approaches might you employ to keep the rabies virus from reaching these islands?

For suggested answers, see Appendix A.

41 Chapter Review

SUMMARY OF KEY CONCEPTS

CONCEPT 41.1

Interactions within a community may help, harm, or have no effect on the species involved (pp. 846–851)

Interaction	Description
Competition (–/–)	Two or more species compete for a resource that is in short supply.
Predation (+/–)	One species, the predator, kills and eats the other, the prey.
Herbivory (+/–)	An herbivore eats part of a plant or alga.
Symbiosis	Individuals of two or more species live in close contact with one another. Symbiosis includes:
Parasitism (+/–)	The **parasite** derives its nourishment from a second organism, its **host**, which is harmed.
Mutualism (+/+)	Both species benefit from the interaction.
Commensalism (+/0)	One species benefits from the interaction, while the other is unaffected by it.
Facilitation (+/+ or 0/+)	A species has positive effects on other species without intimate contact.

- **Competitive exclusion** states that two species competing for the same resources cannot coexist permanently in the same place. **Resource partitioning** is the differentiation of **ecological niches** that enables species to coexist in a community.

? *Give an example of a pair of species that exhibit each interaction listed in the table above.*

CONCEPT 41.2

Diversity and trophic structure characterize biological communities (pp. 851–856)

- **Species diversity** measures the number of species in a community—its **species richness**—and their **relative abundance**. A community with similar abundances of species is more diverse than one in which one or two species are abundant and the remainder are rare.
- **Trophic structure** is a key factor in community dynamics. **Food chains** link the trophic levels in a community. Branching food chains and complex trophic interactions form **food webs**.
- **Dominant species** are the most abundant species in a community and possess high competitive abilities. **Keystone species** are usually less abundant species that exert a disproportionate influence on community structure because of their ecological niche. **Ecosystem engineers** influence community structure through their effects on the physical environment.
- The **bottom-up model** proposes a unidirectional influence from lower to higher trophic levels. **The top-down model** proposes that control of each trophic level comes from the trophic level above.

? *Based on indexes such as Shannon diversity, is a community of higher species richness always more diverse than a community of lower species richness? Explain.*

CONCEPT 41.3

Disturbance influences species diversity and composition (pp. 856–859)

- Increasing evidence suggests that **disturbance** and lack of equilibrium, rather than stability and equilibrium, are the norm for most communities. According to the **intermediate disturbance hypothesis**, moderate levels of disturbance can foster higher species diversity than can low or high levels of disturbance.

- **Ecological succession** is the sequence of community and ecosystem changes after a disturbance. **Primary succession** occurs where no soil exists when succession begins; **secondary succession** begins in an area where soil remains after a disturbance.
- Humans are the most widespread agents of disturbance, and their effects on communities often reduce species diversity.

? *Is the disturbance pictured in Figure 41.20 more likely to initiate primary or secondary succession? Explain.*

CONCEPT 41.4

Biogeographic factors affect community diversity (pp. 859–860)

- Species richness generally declines along a latitudinal gradient from the tropics to the poles. Climate influences the diversity gradient through energy (heat and light) and water.
- Species richness is directly related to a community's geographic size, a principle formalized in the **species-area curve**. The island equilibrium model maintains that species richness on an ecological island reaches an equilibrium where immigration is balanced by extinction.

? *How have periods of glaciation influenced latitudinal patterns of diversity?*

CONCEPT 41.5

Pathogens alter community structure locally and globally (pp. 861–862)

- Recent work has highlighted the role that **pathogens** play in structuring terrestrial and marine communities.
- **Zoonotic pathogens** are transferred from other animals to humans. Community ecology provides the framework for identifying key species interactions associated with such pathogens.

? *In what way can a vector of a zoonotic pathogen differ from a host of the pathogen?*

TEST YOUR UNDERSTANDING

Level 1: Knowledge/Comprehension

1. The feeding relationships among the species in a community determine the community's
   - **a.** secondary succession.
   - **b.** ecological niche.
   - **c.** species richness.
   - **d.** species-area curve.
   - **e.** trophic structure.
2. Based on the intermediate disturbance hypothesis, a community's species diversity is increased by
   - **a.** frequent massive disturbance.
   - **b.** stable conditions with no disturbance.
   - **c.** moderate levels of disturbance.
   - **d.** human intervention to eliminate disturbance.
   - **e.** intensive disturbance by humans.

Level 2: Application/Analysis

3. Which of the following could qualify as a top-down control on a grassland community?
   - **a.** limitation of plant biomass by rainfall amount
   - **b.** influence of temperature on competition among plants
   - **c.** influence of soil nutrients on the abundance of grasses versus wildflowers
   - **d.** effect of grazing intensity by bison on plant species diversity
   - **e.** effect of humidity on plant growth rates
4. Community 1 contains 100 individuals distributed among four species (A, B, C, and D). Community 2 contains 100 individuals distributed among three species (A, B, and C).

   Community 1: 5A, 5B, 85C, 5D
   Community 2: 30A, 40B, 30C

   Calculate the Shannon diversity index (H) for each community. Which community is more diverse?

Level 3: Synthesis/Evaluation

5. **DRAW IT** An important species in the Chesapeake Bay estuary is the blue crab (*Callinectes sapidus*). It is an omnivore, eating eelgrass and other primary producers as well as clams. It is also a cannibal. In turn, the crabs are eaten by humans and by the endangered Kemp's Ridley sea turtle. Based on this information, draw a food web that includes the blue crab. Assuming that the top-down model holds for this system, what would happen to the abundance of eelgrass if humans stopped eating blue crabs?
6. **SCIENTIFIC INQUIRY**
   An ecologist studying plants in the desert performed the following experiment. She staked out two identical plots, each of which included a few sagebrush plants and numerous small annual wildflowers. She found the same five wildflower species in roughly equal numbers on both plots. She then enclosed one of the plots with a fence to keep out kangaroo rats, the most common grain-eaters of the area. After two years, four of the wildflower species were no longer present in the fenced plot, but one species had increased drastically. The control plot had not changed in species diversity. Using the principles of community ecology, propose a hypothesis to explain her results. What additional evidence would support your hypothesis?
7. **FOCUS ON EVOLUTION**
   Explain why adaptations of particular organisms to interspecific competition may not necessarily represent instances of character displacement. What would a researcher have to demonstrate about two competing species to make a convincing case for character displacement?
8. **FOCUS ON INFORMATION**
   In Batesian mimicry, a palatable species resembles an unpalatable one. Imagine that several individuals of a palatable, brightly colored fly species are carried by the wind to three remote islands. The first island has no predators of that species; the second has predators but no similarly colored, unpalatable species; and the third has both predators and a similarly colored, unpalatable species. In a short essay (100–150 words), predict what might happen to the coloration of the palatable species on each island over evolutionary time if coloration is a genetically controlled trait. Explain your predictions.

For selected answers, see Appendix A.

42 Ecosystems and Energy

KEY CONCEPTS

42.1 Physical laws govern energy flow and chemical cycling in ecosystems

42.2 Energy and other limiting factors control primary production in ecosystems

42.3 Energy transfer between trophic levels is typically only 10% efficient

42.4 Biological and geochemical processes cycle nutrients and water in ecosystems

42.5 Restoration ecologists help return degraded ecosystems to a more natural state

▼ **Figure 42.1** Why is this Antarctic ice blood red?

OVERVIEW

Cool Ecosystem

Three hundred meters below Taylor Glacier, in Antarctica, an unusual community of bacteria lives on sulfur- and iron-containing ions. These organisms thrive in harsh conditions, without light or oxygen and at a temperature of –10°C, so low that the water would freeze if it weren't three times as salty as the ocean. How has this community survived, isolated from Earth's surface for at least 1.5 million years? The bacteria are chemoautotrophs, which obtain energy by oxidizing sulfur taken up from their sulfate-rich environment (see Chapter 24). They use iron as a final electron acceptor in their reactions. When the water flows from the base of the glacier and comes into contact with air, the reduced iron in the water is oxidized and turns red before the water freezes. The distinctive color gives this area of the glacier its name—Blood Falls **(Figure 42.1)**.

Together, the bacterial community and surrounding environment make up an **ecosystem**, the sum of all the organisms living in a given area and the abiotic factors with which they interact. An ecosystem can encompass a vast area, such as a lake or forest, or a microcosm, such as the space under a fallen log or a desert spring **(Figure 42.2)**. As with populations and communities, the boundaries of ecosystems are not always discrete. Many ecologists view the entire biosphere as a global ecosystem, a composite of all of the local ecosystems on Earth.

Regardless of an ecosystem's size, two key ecosystem processes cannot be fully described by the population or community phenomena you have studied so far: energy flow and chemical cycling. Energy enters most ecosystems as sunlight. It is converted to chemical energy by autotrophs, passed to heterotrophs in the organic compounds of food, and dissipated as heat. Chemical elements, such as carbon and nitrogen, are cycled among abiotic and biotic components of the ecosystem. Photosynthetic and chemosynthetic organisms take up these elements in inorganic form from the air, soil, and water and incorporate them into their biomass, some of which is consumed by animals. The elements are returned in inorganic form to the environment by the metabolism of plants and animals and by organisms such as bacteria and fungi that break down organic wastes and dead organisms.

▲ **Figure 42.2 A desert spring ecosystem.**

Both energy and matter are transformed in ecosystems through photosynthesis and feeding relationships. But unlike matter, energy cannot be recycled. An ecosystem must be powered by a continuous influx of energy from an external source—in most cases, the sun. Energy flows through ecosystems, whereas matter cycles within and through them.

Resources critical to human survival and welfare, ranging from the food we eat to the oxygen we breathe, are products of ecosystem processes. In this chapter, we'll explore the dynamics of energy flow and chemical cycling, emphasizing the results of ecosystem experiments. One way to study ecosystem processes is to alter environmental factors, such as temperature or the abundance of nutrients, and measure how ecosystems respond. We'll also consider some of the impacts of human activities on energy flow and chemical cycling. Finally, we'll explore the growing science of restoration ecology, which focuses on returning degraded ecosystems to a more natural state.

CONCEPT 42.1

Physical laws govern energy flow and chemical cycling in ecosystems

Cells transform energy and matter, subject to the laws of thermodynamics (see Concept 6.1). Like cell biologists, ecosystem ecologists study how energy and matter are transformed within a system and measure the amounts of both that cross the system's boundaries. By grouping the species in a community into trophic levels based on feeding relationships (see Concept 41.2), we can follow the transformations of energy in an ecosystem and map the movements of chemical elements.

Conservation of Energy

Because ecosystem ecologists study the interactions of organisms with the physical environment, many ecosystem approaches are based on laws of physics and chemistry. The first law of thermodynamics states that energy cannot be created or destroyed but only transferred or transformed. Plants and other photosynthetic organisms convert solar energy to chemical energy, but the total amount of energy does not change. The amount of energy stored in organic molecules must equal the total solar energy intercepted by the plant, minus the amounts reflected and dissipated as heat. Ecosystem ecologists often measure transfers within and across ecosystems, in part to understand how many organisms a habitat can support and how much food humans can harvest from a site.

One implication of the second law of thermodynamics, which states that every exchange of energy increases the entropy of the universe, is that energy conversions are inefficient. Some energy is always lost as heat. We can measure the efficiency of ecological energy conversions just as we measure the efficiency of light bulbs and car engines. Because the energy flowing through ecosystems is ultimately dissipated into space as heat, most ecosystems would vanish if the sun were not continuously providing energy to Earth.

Conservation of Mass

Matter, like energy, cannot be created or destroyed. This **law of conservation of mass** is as important for ecosystems as the laws of thermodynamics are. Because mass is conserved, we can determine how much of a chemical element cycles within an ecosystem or is gained or lost by that ecosystem over time.

Unlike energy, chemical elements are continually recycled within ecosystems. A carbon atom in CO_2 can be released from the soil by a decomposer, taken up by grass through photosynthesis, consumed by a bison or other grazer, and returned to the soil in the bison's waste. The measurement and analysis of chemical cycling are important aspects of ecosystem ecology.

Although most elements are not gained or lost on a global scale, they can be gained by or lost from a particular ecosystem. In a forest, mineral nutrients—the essential elements that plants obtain from soil—typically enter as dust or as solutes dissolved in rainwater or leached from rocks in the ground. Nitrogen is also supplied through the biological process of nitrogen fixation (see Figure 29.11). In terms of losses, some elements return to the atmosphere as gases, and others are carried out of the ecosystem by moving water or by wind. Like organisms, ecosystems are open systems, absorbing energy and mass and releasing heat and waste products.

In nature, most gains and losses to ecosystems are small compared to the amounts recycled within them. Still, the balance between inputs and outputs determines whether an ecosystem is a source or a sink for a given element. If a mineral nutrient's outputs exceed its inputs, it will eventually limit production in that system. Human activities often change the balance of inputs and outputs considerably, as we'll see later in this chapter.

Energy, Mass, and Trophic Levels

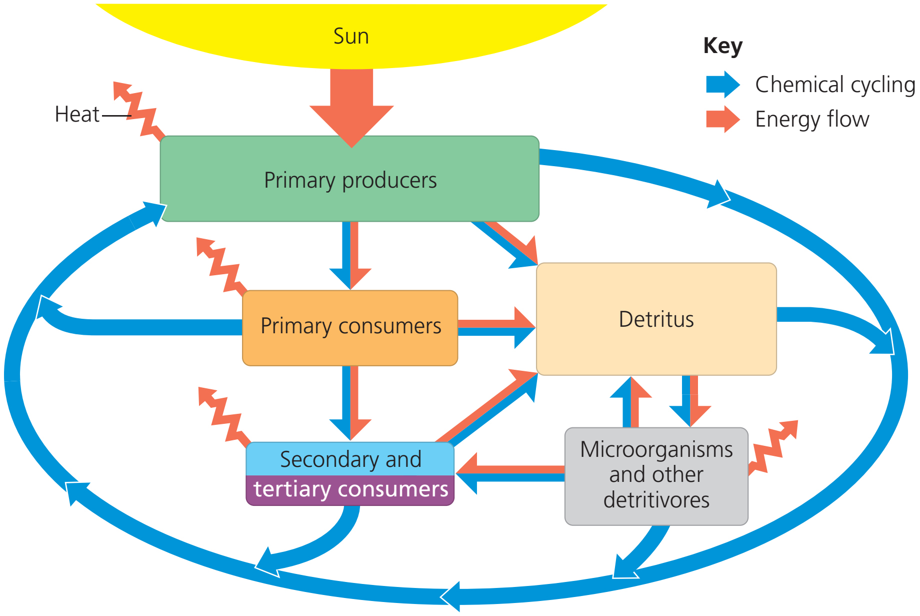
Ecologists group species into trophic levels based on their main source of nutrition and energy (see Concept 41.2). The trophic level that ultimately supports all others consists of autotrophs, also called the **primary producers** of the ecosystem. Most autotrophs are photosynthetic organisms that use light energy to synthesize sugars and other organic compounds, which they then use as fuel for cellular respiration and as building material for growth. Plants, algae, and photosynthetic prokaryotes are the most common autotrophs, although chemosynthetic prokaryotes are the primary producers in deep-sea hydrothermal vents (see Figure 40.10) and places deep underground or beneath ice (see Figure 42.1).

Organisms in trophic levels above the primary producers are heterotrophs, which depend directly or indirectly on the primary producers for their source of energy. Herbivores, which eat plants and other primary producers, are **primary consumers**. Carnivores that eat herbivores are **secondary consumers**, and carnivores that eat other carnivores are **tertiary consumers**.

Another group of heterotrophs is the **detritivores**, or **decomposers**, terms we use synonymously in this text to refer to consumers that get their energy from detritus. **Detritus** is nonliving organic material, such as the remains of dead organisms, feces, fallen leaves, and wood. Many detritivores are in turn eaten by secondary and tertiary consumers. Two important groups of detritivores are prokaryotes and fungi **(Figure 42.3)**. These organisms secrete enzymes that digest organic material; they then absorb the breakdown products, linking the consumers and primary producers in an ecosystem. In a forest, for instance, birds eat earthworms that have been feeding on leaf litter and its associated prokaryotes and fungi.

▲ **Figure 42.3 Fungi decomposing a dead tree.**

Detritivores also play a critical role in recycling chemical elements back to primary producers. Detritivores convert organic matter from all trophic levels to inorganic compounds usable by primary producers, closing the loop of an ecosystem's chemical cycling. Producers can then recycle these elements into organic compounds. If decomposition stopped, life would cease as detritus piled up and the supply of ingredients needed to synthesize new organic matter was exhausted. **Figure 42.4** summarizes the trophic relationships in an ecosystem.



▲ **Figure 42.4 An overview of energy and nutrient dynamics in an ecosystem.** Energy enters, flows through, and exits an ecosystem, whereas chemical nutrients cycle primarily within it. In this generalized scheme, energy (dark orange arrows) enters from the sun as radiation, moves as chemical energy transfers through the food web, and exits as heat radiated into space. Most transfers of nutrients (blue arrows) through the trophic levels lead eventually to detritus; the nutrients then cycle back to the primary producers.

CONCEPT CHECK 42.1

1. Why is the transfer of energy in an ecosystem referred to as energy flow, not energy cycling?
2. **WHAT IF?** You are studying nitrogen cycling on the Serengeti Plain in Africa. During your experiment, a herd of migrating wildebeests grazes through your study plot. What would you need to know to measure their effect on nitrogen balance in the plot?
3. **MAKE CONNECTIONS** How does the second law of thermodynamics explain why an ecosystem's energy supply must be continually replenished? (See Concept 6.1 to review the laws of thermodynamics.)

For suggested answers, see Appendix A.

CONCEPT 42.2

Energy and other limiting factors control primary production in ecosystems

The theme of energy transfer underlies all biological interactions (see Chapter 1). In most ecosystems, the amount of light energy converted to chemical energy—in the form of organic compounds—by autotrophs during a given time period is the ecosystem's **primary production**. These photosynthetic products are the starting point for most studies of ecosystem metabolism and energy flow. In ecosystems where the primary producers are chemoautotrophs, as described in the Overview, the initial energy input is chemical, and the initial products are the organic compounds synthesized by the microorganisms.

Ecosystem Energy Budgets

Since most primary producers use light energy to synthesize energy-rich organic molecules, consumers acquire their organic fuels secondhand (or even third- or fourthhand) through food webs (see Figure 41.14). Therefore, the total amount of photosynthetic production sets the spending limit for the entire ecosystem's energy budget.

The Global Energy Budget

Each day, Earth's atmosphere is bombarded by about 10^{22} joules of solar radiation (1 J = 0.239 cal). This is enough energy to supply the demands of the entire human population for approximately 20 years at 2010 energy consumption levels. The intensity of the solar energy striking Earth varies with latitude, with the tropics receiving the greatest input (see Figure 40.3). Most incoming solar radiation is absorbed, scattered, or reflected by clouds and dust in the atmosphere. The amount of solar radiation that ultimately reaches Earth's surface limits the possible photosynthetic output of ecosystems.

Only a small fraction of the sunlight that reaches Earth's surface is actually used in photosynthesis. Much of the radiation strikes materials that don't photosynthesize, such as ice and soil. Of the radiation that does reach photosynthetic organisms, only certain wavelengths are absorbed by photosynthetic pigments (see Figure 8.9); the rest is transmitted, reflected, or lost as heat. As a result, only about 1% of the visible light that strikes photosynthetic organisms is converted to chemical energy. Nevertheless, Earth's primary producers create about 150 billion metric tons (1.50×10^{14} kg) of organic material each year.

Gross and Net Production

Total primary production in an ecosystem is known as that ecosystem's **gross primary production (GPP)**—the amount of energy from light (or chemicals, in chemoautotrophic systems) converted to the chemical energy of organic molecules per unit time. Not all of this production is stored as organic material in the primary producers because they use some of the molecules as fuel in their own cellular respiration. **Net primary production (NPP)** is equal to gross primary production minus the energy used by the primary producers for their "autotrophic respiration" (R_a):

$$NPP = GPP - R_a$$

On average, NPP is about one-half of GPP. To ecologists, NPP is the key measurement because it represents the storage of chemical energy that will be available to consumers in the ecosystem.

Net primary production can be expressed as energy per unit area per unit time ($J/m^2 \cdot yr$) or as biomass (mass of vegetation) added per unit area per unit time ($g/m^2 \cdot yr$). (Note that biomass is usually expressed in terms of the dry mass of organic material.) An ecosystem's NPP should not be confused with the total biomass of photosynthetic autotrophs present, a measure called the *standing crop*. Net primary production is the amount of *new* biomass added in a given period of time. Although a forest has a large standing crop, its NPP may actually be less than that of some grasslands; grasslands do not accumulate as much biomass as forests because animals consume the plants rapidly and because grasses and herbs decompose more quickly than trees do.

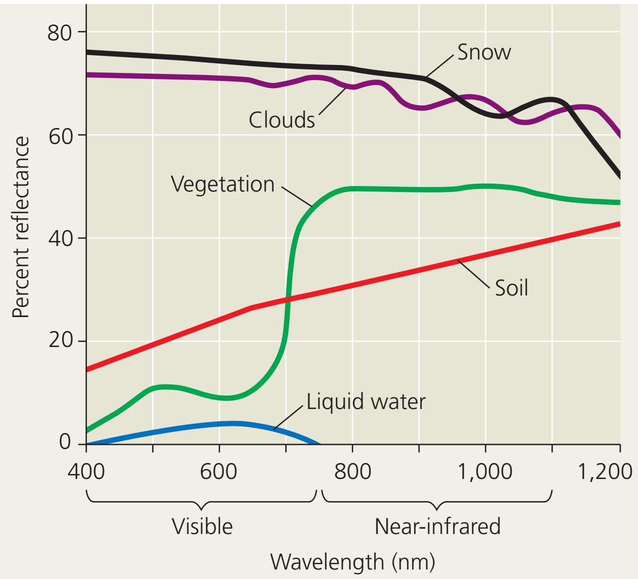
Satellites provide a powerful tool for studying global patterns of primary production **(Figure 42.5)**. Images produced from satellite data show that different ecosystems vary considerably in their NPP. Tropical rain forests are among the most productive terrestrial ecosystems and contribute a large portion of the planet's NPP. Estuaries and coral reefs also have

▼ Figure 42.5 Research Method

Determining Primary Production with Satellites

Application Because chlorophyll captures visible light (see Figure 8.9), photosynthetic organisms absorb more light at visible wavelengths (about 380–750 nm) than at near-infrared wavelengths (750–1,100 nm). Scientists use this difference in absorption to estimate the rate of photosynthesis in different regions of the globe using satellites.

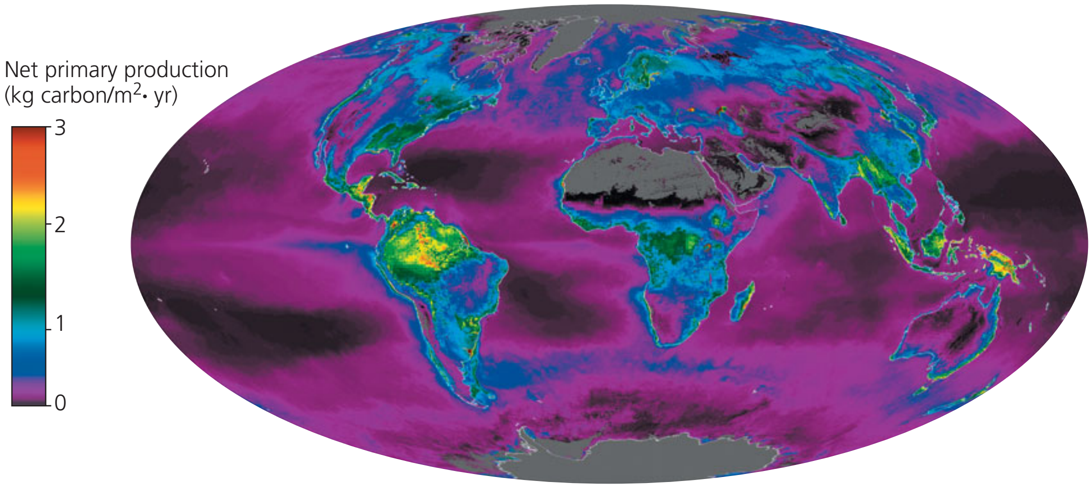
Technique Most satellites determine what they "see" by comparing the ratios of wavelengths reflected back to them. Vegetation reflects much more near-infrared radiation than visible radiation, producing a reflectance pattern very different from that of snow, clouds, soil, and liquid water.



Results Scientists use the satellite data to help produce maps of primary production like the one in Figure 42.6.

▶ **Figure 42.6 Global net primary production.** This map is based on data collected by satellites, such as amount of sunlight absorbed by vegetation. Note that tropical land areas have the highest rates of production (yellow and red on the map).

? *Does this global map accurately illustrate the importance of some highly productive habitats, such as wetlands, coral reefs, and coastal zones? Explain.*



very high NPP, but their contribution to the global total is small because these ecosystems cover only about one-tenth the area covered by tropical rain forests. In contrast, while the open oceans are relatively unproductive **(Figure 42.6)**, their vast size means that together they contribute about as much global NPP as terrestrial systems do.

Whereas NPP can be stated as the amount of new biomass added in a given period of time, **net ecosystem production (NEP)** is a measure of the *total biomass accumulation* during that time. Net ecosystem production is defined as gross primary production minus the total respiration of all organisms in the system (R_T)—not just primary producers, as for the calculation of NPP, but decomposers and other heterotrophs as well:

$$NEP = GPP - R_T$$

NEP is useful to ecologists because its value determines whether an ecosystem is gaining or losing carbon over time. A forest may have a positive NPP but still lose carbon if heterotrophs release it as CO_2 more quickly than primary producers incorporate it into organic compounds.

The most common way to estimate NEP is to measure the net flux (flow) of CO_2 or O_2 entering or leaving the ecosystem. If more CO_2 enters than leaves, the system is storing carbon. Because O_2 release is directly coupled to photosynthesis and respiration (see Figure 7.2), a system that is giving off O_2 is also storing carbon. On land, ecologists typically measure only the net flux of CO_2 from ecosystems because detecting small changes in O_2 in a large atmospheric O_2 pool is difficult. In the oceans, researchers use both approaches.

What limits production in ecosystems? To ask this question another way, what factors could we change to increase production for a given ecosystem? We'll address this question first for aquatic ecosystems.

Primary Production in Aquatic Ecosystems

In aquatic (marine and freshwater) ecosystems, both light and nutrients are important in controlling primary production.

Light Limitation

Because solar radiation drives photosynthesis, you would expect light to be a key variable in controlling primary production in oceans. Indeed, the depth of light penetration affects primary production throughout the photic zone of an ocean or lake (see Figure 40.11). About half of the solar radiation is absorbed in the first 15 m of water. Even in "clear" water, only 5–10% of the radiation may reach a depth of 75 m.

If light were the main variable limiting primary production in the ocean, we would expect production to increase along a gradient from the poles toward the equator, which receives the greatest intensity of light. However, you can see in Figure 42.6 that there is no such gradient. Another factor must strongly influence primary production in the ocean.

Nutrient Limitation

More than light, nutrients limit primary production in most oceans and lakes. A **limiting nutrient** is the element that must be added for production to increase. The nutrient most often limiting marine production is either nitrogen or phosphorus. Concentrations of these nutrients are typically low in the photic zone because they are rapidly taken up by phytoplankton and because detritus tends to sink.

As detailed in **Figure 42.7**, nutrient enrichment experiments confirmed that nitrogen was limiting phytoplankton growth off the south shore of Long Island, New York. One practical application of this work is in preventing algal "blooms" caused by excess nitrogen runoff that fertilizes the phytoplankton. Prior to this research, phosphate contamination was thought to cause many such blooms in the ocean, but eliminating phosphates alone may not help unless nitrogen pollution is also controlled.

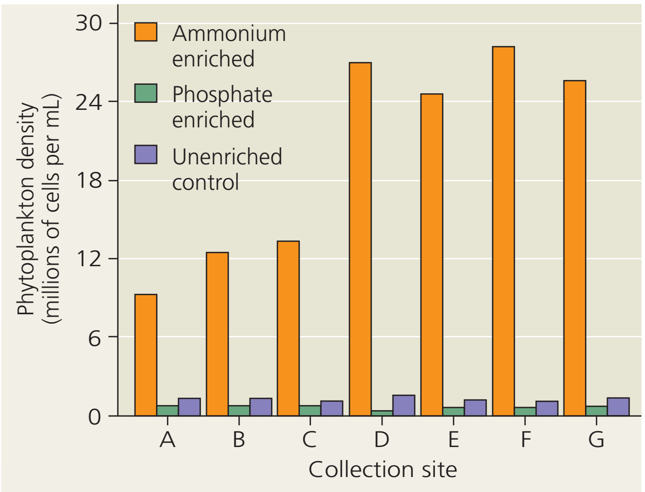
The macronutrients nitrogen and phosphorus are not the only nutrients that limit aquatic production. Several large areas of the ocean have low phytoplankton densities despite relatively high nitrogen concentrations. The Sargasso Sea,

▼ Figure 42.7 Inquiry

Which nutrient limits phytoplankton production along the coast of Long Island?

Experiment Pollution from duck farms concentrated near Moriches Bay adds both nitrogen and phosphorus to the coastal water off Long Island, New York. To determine which nutrient limits phytoplankton growth in this area, John Ryther and William Dunstan, of the Woods Hole Oceanographic Institution, cultured the phytoplankton *Nannochloris atomus* with water collected from several sites, identified as A–G. They added either ammonium (NH_4^+) or phosphate (PO_4^{3-}) to some of the cultures.

Results The addition of ammonium caused heavy phytoplankton growth in the cultures, but the addition of phosphate did not.



Conclusion Since adding phosphorus, which was already in rich supply, did not increase *Nannochloris* growth, whereas adding nitrogen increased phytoplankton density dramatically, the researchers concluded that nitrogen is the nutrient that limits phytoplankton growth in this ecosystem.

Source J. H. Ryther and W. M. Dunstan, Nitrogen, phosphorus, and eutrophication in the coastal marine environment, *Science* 171:1008–1013 (1971).

WHAT IF? How would you expect the results of this experiment to change if new duck farms substantially increased the amount of pollution in the water? Explain your reasoning.

a subtropical region of the Atlantic Ocean, has some of the clearest water in the world because of its low phytoplankton density. Nutrient enrichment experiments have revealed that the availability of the micronutrient iron limits primary production there **(Table 42.1)**. Windblown dust from land supplies most of the iron to the oceans but is relatively scarce in this and certain other regions compared to the oceans as a whole.

Areas of *upwelling*, where deep, nutrient-rich waters circulate to the ocean surface, have exceptionally high primary production. This fact supports the hypothesis that nutrient availability determines marine primary production. Because upwelling stimulates growth of the phytoplankton that form the base of marine food webs, upwelling areas typically host highly productive, diverse ecosystems and are prime fishing locations. The largest areas of upwelling occur in the Southern Ocean (also called the Antarctic Ocean), along the equator, and in the coastal waters off Peru, California, and parts of western Africa.

Table 42.1 Nutrient Enrichment Experiment for Sargasso Sea Samples

Nutrients Added to Experimental Culture	Relative Uptake of ^{14}C by Cultures*
None (controls)	1.00
Nitrogen (N) + phosphorus (P) only	1.10
N + P + metals (excluding iron)	1.08
N + P + metals (including iron)	12.90
N + P + iron	12.00

*^{14}C uptake by cultures measures primary production.

Source D. W. Menzel and J. H. Ryther, Nutrients limiting the production of phytoplankton in the Sargasso Sea, with special reference to iron, *Deep Sea Research* 7:276–281 (1961).

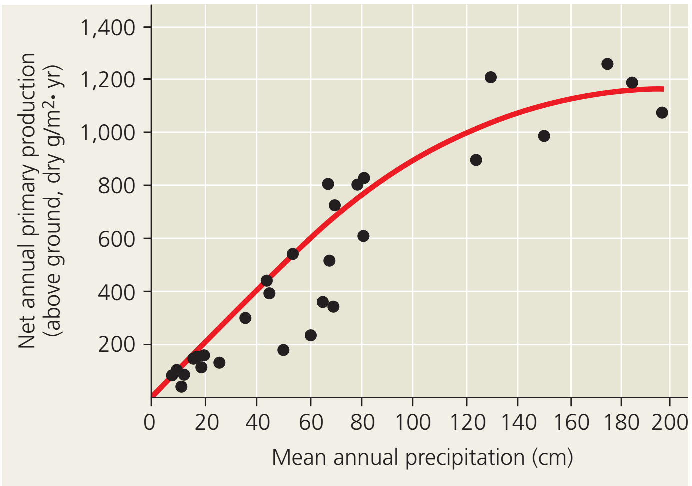
In freshwater lakes, nutrient limitation is also common. During the 1970s, scientists showed that sewage and fertilizer runoff from farms and lawns adds large amounts of nutrients to lakes. Cyanobacteria and algae grow rapidly in response to these added nutrients. When the primary producers die, detritivores can reduce or even use up the available oxygen in the water through decomposition, also reducing the clarity of the water. The ecological impacts of this process, known as **eutrophication** (from the Greek *eutrophos*, well nourished), include the loss of many fish species from the lakes (see Figure 40.10).

Controlling eutrophication requires knowing which polluting nutrient is responsible. While nitrogen rarely limits primary production in lakes, a series of whole-lake experiments showed that phosphorus availability limits cyanobacterial growth. This and other ecological research led to the use of phosphate-free detergents and other important water quality reforms.

Primary Production in Terrestrial Ecosystems

At regional and global scales, temperature and moisture are the main factors controlling primary production in terrestrial ecosystems. Tropical rain forests, with their warm, wet conditions that promote plant growth, are the most productive of all terrestrial ecosystems (see Figure 42.6). In contrast, low-productivity systems are generally hot and dry, like many deserts, or cold and dry, like arctic tundra. Between these extremes lie the temperate forest and grassland ecosystems, which have moderate climates and intermediate productivity.

The climate variables of moisture and temperature are very useful for predicting NPP in terrestrial ecosystems. Primary production is greater in wetter ecosystems, as shown for the



▲ **Figure 42.8 A global relationship between net primary production and mean annual precipitation for terrestrial ecosystems.**

plot of NPP and annual precipitation in **Figure 42.8**. Along with mean annual precipitation, a second useful predictor is *actual evapotranspiration*, the total amount of water transpired by plants and evaporated from a landscape. Evapotranspiration increases with the temperature and amount of solar energy available to drive evaporation and transpiration.

Nutrient Limitations and Adaptations That Reduce Them

EVOLUTION Mineral nutrients in the soil also limit primary production in terrestrial ecosystems. As in aquatic systems, nitrogen and phosphorus are the nutrients that most commonly limit terrestrial production. Globally, nitrogen limits plant growth most. Phosphorus limitations are common in older soils where phosphate molecules have been leached away by water, such as in many tropical ecosystems. Phosphorus availability is also often low in the soils of deserts and other ecosystems with a basic pH, where some phosphorus precipitates and becomes unavailable to plants. Adding a nonlimiting nutrient, even one that is scarce, will not stimulate production. Conversely, adding more of the limiting nutrient will increase production until some other nutrient becomes limiting.

Various adaptations have evolved in plants that can increase their uptake of limiting nutrients. One important adaptation is the symbiosis between plant roots and nitrogen-fixing bacteria. Another is the mycorrhizal association between plant roots and fungi that supply phosphorus and other limiting elements to plants (see Concept 29.4). Plants also have root hairs and other anatomical features that increase their area of contact with the soil (see Chapter 28). Many plants release enzymes and other substances into the soil that increase the availability of limiting nutrients; such enzymes include phosphatases, which cleave a phosphate group from larger molecules and make it more soluble in the soil.

Studies relating nutrients to terrestrial primary production have practical applications in agriculture. Farmers maximize their crop yields by using fertilizers with the right balance of nutrients for the local soil and type of crop. This knowledge of limiting nutrients helps us feed billions of people today.

CONCEPT CHECK 42.2

1. Why is only a small portion of the solar energy that strikes Earth's atmosphere stored by primary producers?
2. How can ecologists experimentally determine the factor that limits primary production in an ecosystem?
3. **MAKE CONNECTIONS** Explain how nitrogen and phosphorus, the nutrients that most often limit primary production, are necessary for the Calvin cycle to function in photosynthesis (see Concept 8.3).

For suggested answers, see Appendix A.

CONCEPT 42.3

Energy transfer between trophic levels is typically only 10% efficient

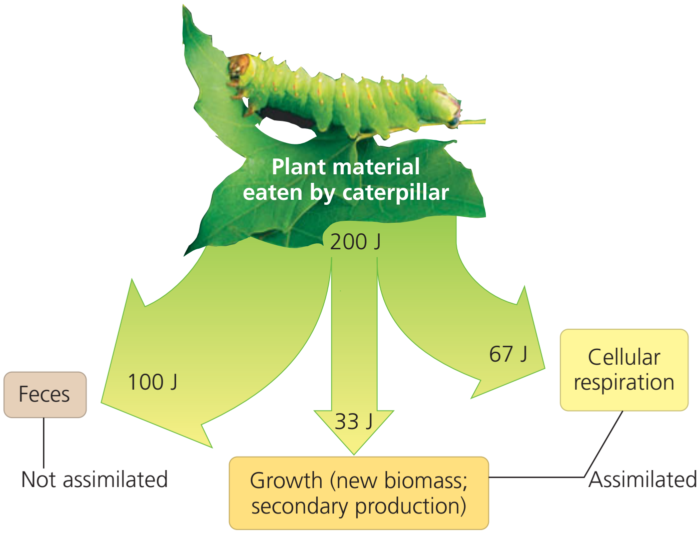
The amount of chemical energy in consumers' food that is converted to new biomass during a given period is called the **secondary production** of the ecosystem. Consider the transfer of organic matter from primary producers to herbivores, the primary consumers. In most ecosystems, herbivores eat only a small fraction of plant material produced; globally, they consume only about one-sixth of total plant production. Moreover, they cannot digest all the plant material that they *do* eat, as anyone who has walked through a dairy farm will attest. Most of an ecosystem's production is eventually consumed by detritivores. Let's analyze the process of energy transfer and cycling more closely.

Production Efficiency

First we'll examine secondary production in one organism—a caterpillar. When a caterpillar feeds on a leaf, only about 33 J out of 200 J, or one-sixth of the potential energy in the leaf, is used for secondary production, or growth **(Figure 42.9)**. The caterpillar stores some of the remaining energy in organic compounds that will be used for cellular respiration and passes the rest in its feces. Most of the energy in feces is eventually lost as heat after the feces are consumed by detritivores. The energy used for the caterpillar's respiration is also lost from the ecosystem as heat. This is why energy is said to flow through, not cycle within, ecosystems. Only the chemical energy stored by herbivores as biomass, through growth or the production of offspring, is available as food to secondary consumers.

We can measure the efficiency of animals as energy transformers using the following equation:

$$\text{Production efficiency} = \frac{\text{Net secondary production} \times 100\%}{\text{Assimilation of primary production}}$$



▲ **Figure 42.9 Energy partitioning within a link of the food chain.** Less than 17% of the caterpillar's food is actually used for secondary production (growth).

Net secondary production is the energy stored in biomass represented by growth and reproduction. Assimilation consists of the total energy taken in, not including losses in feces, used for growth, reproduction, and respiration. **Production efficiency**, therefore, is the percentage of energy stored in assimilated food that is *not* used for respiration. For the caterpillar in Figure 42.9, production efficiency is 33%; 67 J of the 100 J of assimilated energy is used for respiration. (The 100 J of energy lost as undigested material in feces does not count toward assimilation.) Birds and mammals typically have low production efficiencies, in the range of 1–3%, because they use so much energy in maintaining a constant, high body temperature. Insects and microorganisms are much more efficient, with production efficiencies averaging 40% or more.

Trophic Efficiency and Ecological Pyramids

Let's scale up now from the production efficiencies of individual consumers to the flow of energy through trophic levels.

Trophic efficiency is the percentage of production transferred from one trophic level to the next. Trophic efficiencies must always be less than production efficiencies because they take into account not only the energy lost through respiration and contained in feces, but also the energy in organic material in a lower trophic level that is not consumed by the next trophic level. Trophic efficiencies are generally only about 10%. In other words, 90% of the energy available at one trophic level typically is *not* transferred to the next. This loss is multiplied over the length of a food chain. For example, if 10% of available energy is transferred from primary producers to primary consumers, such as caterpillars, and 10% of that energy is transferred to secondary consumers, called carnivores, then only 1% of net primary production is available to secondary consumers (10% of 10%). In the **Scientific Skills Exercise**, you can calculate trophic efficiency and other measures of energy flow in a salt marsh ecosystem.

The progressive loss of energy along a food chain severely limits the abundance of top-level carnivores that an ecosystem can support. Only about 0.1% of the chemical energy fixed by photosynthesis can flow all the way through a food web to a tertiary consumer, such as a snake or a shark. This explains why most food webs include only about four or five trophic levels (see Chapter 41).

The loss of energy with each transfer in a food chain can be represented by a *pyramid of net production*, in which the

Scientific Skills Exercise

Interpreting Quantitative Data in a Table

How Efficient Is Energy Transfer in a Salt Marsh Ecosystem? In a classic experiment, John Teal studied the flow of energy through the producers, consumers, and detritivores in a salt marsh. In this exercise, you will use the data from this study to calculate some measures of energy transfer between trophic levels in this ecosystem.

How the Study Was Done Teal measured the amount of solar radiation entering a salt marsh in Georgia over a year. He also measured the aboveground biomass of the dominant primary producers, which were grasses, as well as the biomass of the dominant consumers, including insects, spiders, and crabs, and of the detritus that flowed out of the marsh to the surrounding coastal waters. To determine the amount of energy in each unit of biomass, he dried the biomass, burned it in a calorimeter, and measured the amount of heat produced.

Data from the Study

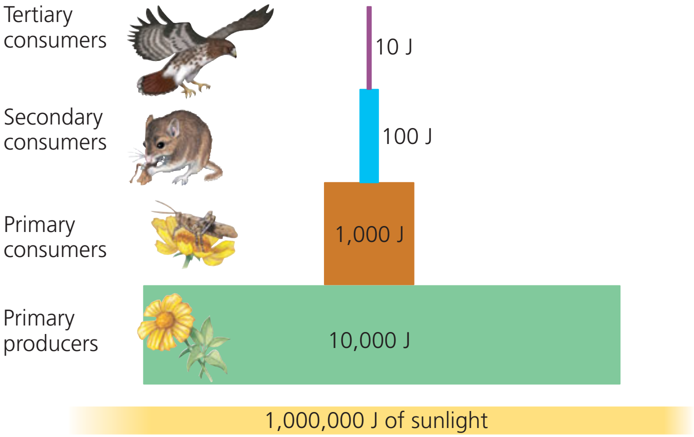
Form of Energy	$kcal/m^2 \cdot yr$
Solar radiation	600,000
Gross grass production	34,580
Net grass production	6,585
Gross insect production	305
Net insect production	81
Detritus leaving marsh	3,671

Interpret the Data

1. What proportion of the solar energy that reaches the marsh is incorporated into gross primary production? Into net primary production? (A proportion is the same as a percentage divided by 100. Both measures are useful for comparing relative efficiencies across different ecosystems.)
2. How much energy is lost by primary producers as respiration in this ecosystem? How much is lost as respiration by the insect population?
3. If all of the detritus leaving the marsh is plant material, what proportion of all net primary production leaves the marsh as detritus each year?

Data from J. M. Teal, Energy flow in the salt marsh ecosystem of Georgia, *Ecology* 43:614–624 (1962).

MB A version of this Scientific Skills Exercise can be assigned in MasteringBiology.



▲ **Figure 42.10 An idealized pyramid of net production.** This example assumes a trophic efficiency of 10% for each link in the food chain. Notice that primary producers convert only about 1% of the energy available to them to net primary production.

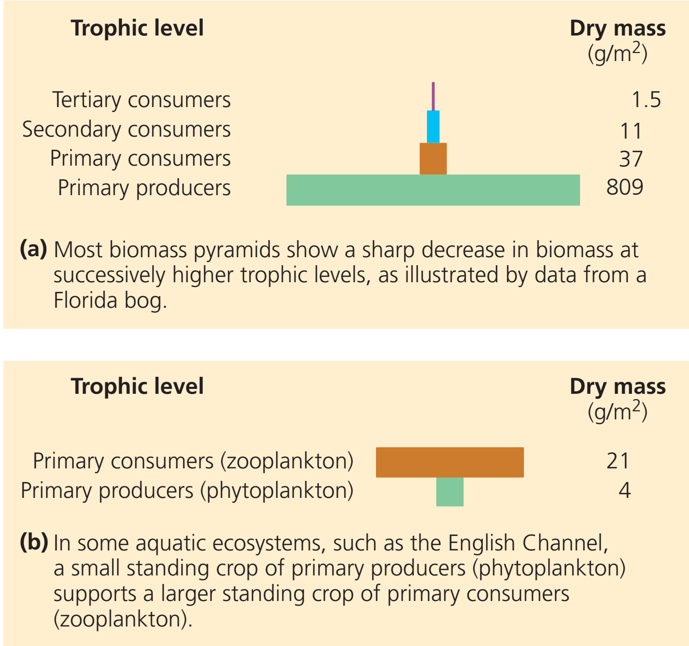
trophic levels are arranged in tiers **(Figure 42.10)**. The width of each tier is proportional to the net production, expressed in joules, of each trophic level. The highest level, which represents top-level predators, contains relatively few individuals. The small population size typical of top predator species is one reason they tend to be vulnerable to extinction (as well as to the evolutionary consequences of small population size, discussed in Concept 21.3).

One important ecological consequence of low trophic efficiencies is represented in a *biomass pyramid*, in which each tier represents the standing crop (the total dry mass of all organisms) in one trophic level. Most biomass pyramids narrow sharply from primary producers at the base to top-level carnivores at the apex because energy transfers between trophic levels are so inefficient **(Figure 42.11a)**. Certain aquatic ecosystems, however, have inverted biomass pyramids: Primary consumers outweigh the producers **(Figure 42.11b)**. Such inverted biomass pyramids occur because the producers—phytoplankton—grow, reproduce, and are consumed so quickly by the zooplankton that they never develop a large population size, or standing crop. In other words, the phytoplankton have a short **turnover time**, which means they have a small standing crop compared to their production:

$$\text{Turnover time} = \frac{\text{Standing crop (g/m}^2\text{)}}{\text{Production (g/m}^2 \cdot \text{day)}}$$

Because the phytoplankton continually replace their biomass at such a rapid rate, they can support a biomass of zooplankton bigger than their own biomass. Nevertheless, because phytoplankton have much higher production than zooplankton, the pyramid of *production* for this ecosystem is still bottom-heavy, like the one in Figure 42.10.

The dynamics of energy flow through ecosystems have important implications for human consumers. Eating meat is a relatively inefficient way of tapping photosynthetic production. The same pound of soybeans that a person could eat for



(a) Most biomass pyramids show a sharp decrease in biomass at successively higher trophic levels, as illustrated by data from a Florida bog.

(b) In some aquatic ecosystems, such as the English Channel, a small standing crop of primary producers (phytoplankton) supports a larger standing crop of primary consumers (zooplankton).

▲ **Figure 42.11 Pyramids of biomass (standing crop).** Numbers denote the dry mass of all organisms at each trophic level.

protein produces only a fifth of a pound of beef or less when fed to a cow. Worldwide agriculture could, in fact, feed many more people and require less land if we all fed more efficiently—as primary consumers, eating plant material.

In the next section, we'll look at how the transfer of nutrients and energy through food webs is part of a larger picture of chemical cycling in ecosystems.

CONCEPT CHECK 42.3

1. If an insect that eats plant seeds containing 100 J of energy uses 30 J of that energy for respiration and excretes 50 J in its feces, what is the insect's net secondary production? What is its production efficiency?
2. Tobacco leaves contain nicotine, a poisonous compound that is energetically expensive for the plant to make. What advantage might the plant gain by using some of its resources to produce nicotine?
3. **WHAT IF?** Detritivores are consumers that obtain their energy from detritus. How many joules of energy are potentially available to detritivores in the ecosystem represented in Figure 42.10?

For suggested answers, see Appendix A.

CONCEPT 42.4

Biological and geochemical processes cycle nutrients and water in ecosystems

Although most ecosystems receive abundant solar energy, chemical elements are available only in limited amounts. Life therefore depends on the recycling of essential chemical elements. Much of an organism's chemical stock is replaced continuously as nutrients are assimilated and waste products are released. When the organism dies, the atoms in its body are returned to the atmosphere, water, or soil by decomposers. Decomposition replenishes the pools of inorganic nutrients that plants and other autotrophs use to build new organic matter.

Decomposition and Nutrient Cycling Rates

Decomposition is controlled by the same factors that limit primary production in aquatic and terrestrial ecosystems (see Concept 42.2). These factors include temperature, moisture, and nutrient availability. Decomposers usually grow faster and decompose material more quickly in warmer ecosystems **(Figure 42.12)**. In tropical rain forests, most organic material decomposes in a few months to a few years, while in temperate forests, decomposition takes four to six years, on average. The difference is largely the result of the higher temperatures and more abundant precipitation in tropical rain forests.

Because decomposition in a tropical rain forest is rapid, relatively little organic material accumulates as leaf litter on the forest floor; about 75% of the nutrients in the ecosystem is present in the woody trunks of trees, and only about 10% is contained in the soil. Thus, the relatively low concentrations of some nutrients in the soil of tropical rain forests result from a short cycling time, not from a lack of these elements in the ecosystem. In temperate forests, where decomposition is much slower, the soil may contain as much as 50% of all the organic material in the ecosystem. The nutrients that are present in temperate forest detritus and soil may remain there for long periods before plants assimilate them.

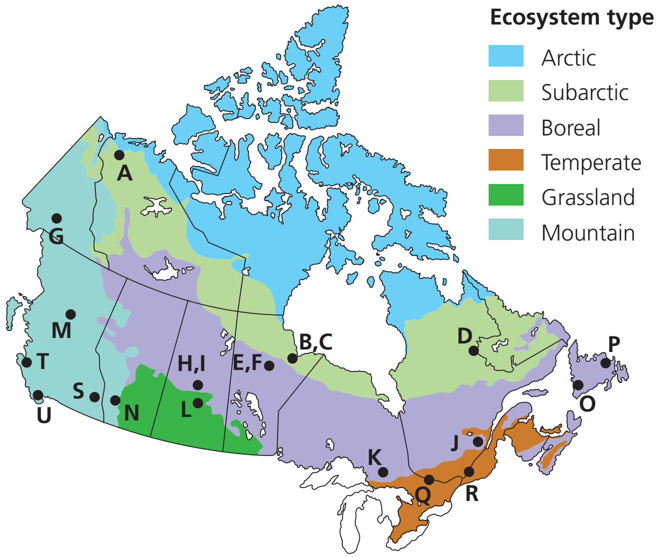
Decomposition on land is also slower when conditions are either too dry for decomposers to thrive or too wet to supply them with enough oxygen. Ecosystems that are both cold and wet, such as peatlands, store large amounts of organic matter. Decomposers grow poorly there, and net primary production greatly exceeds decomposition.

In aquatic ecosystems, decomposition in anaerobic muds can take 50 years or longer. Bottom sediments are comparable to the detritus layer in terrestrial ecosystems; however, algae and aquatic plants usually assimilate nutrients directly from the water. Thus, the sediments often constitute a nutrient sink, and aquatic ecosystems are very productive only when there is exchange between the bottom layers of water and the water at the surface.

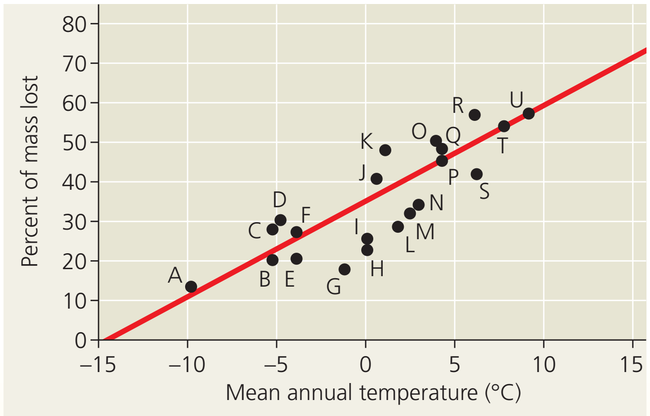
▼ **Figure 42.12 Inquiry**

How does temperature affect litter decomposition in an ecosystem?

Experiment Researchers with the Canadian Forest Service placed identical samples of organic material—litter—on the ground in 21 sites across Canada (marked by letters on the map below). Three years later, they returned to see how much of each sample had decomposed.



Results The mass of litter decreased four times faster in the warmest ecosystem than in the coldest ecosystem.



Conclusion Decomposition rate increases with temperature across much of Canada.

Source T. R. Moore et al., Litter decomposition rates in Canadian forests, *Global Change Biology* 5:75–82 (1999).

WHAT IF? What factors other than temperature might also have varied across these 21 sites? How might this variation have affected the interpretation of the results?

Biogeochemical Cycles

Because nutrient cycles involve both biotic and abiotic components, they are called **biogeochemical cycles**. For convenience, we can recognize two general categories of biogeochemical cycles: global and local. Gaseous forms of carbon, oxygen, sulfur, and nitrogen occur in the atmosphere, and cycles of these elements are essentially global. Other elements, including phosphorus, potassium, and calcium, are too heavy to occur as gases at Earth's surface. They cycle locally in terrestrial ecosystems and more broadly in aquatic ecosystems.

Figure 42.13 provides a detailed look at the cycling of water, carbon, nitrogen, and phosphorus. When you study each

▼ Figure 42.13 Exploring Water and Nutrient Cycling

Examine each cycle closely, considering the major reservoirs of water, carbon, nitrogen, and phosphorus and the processes that drive each cycle. The widths of the arrows in the diagrams approximately reflect the relative contribution of each process to the movement of water or a nutrient in the biosphere.

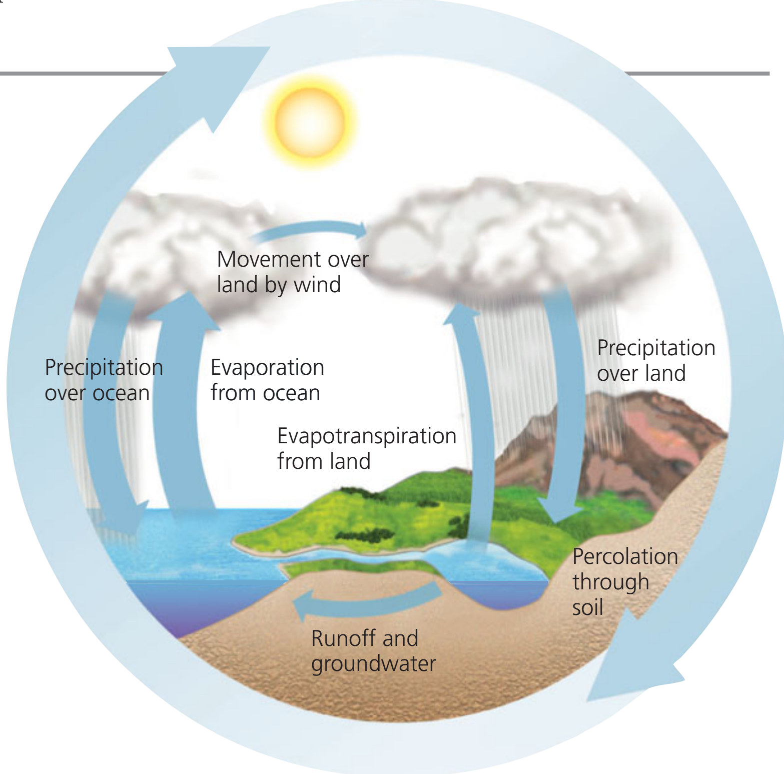
The Water Cycle

Biological importance Water is essential to all organisms, and its availability influences the rates of ecosystem processes, particularly primary production and decomposition in terrestrial ecosystems.

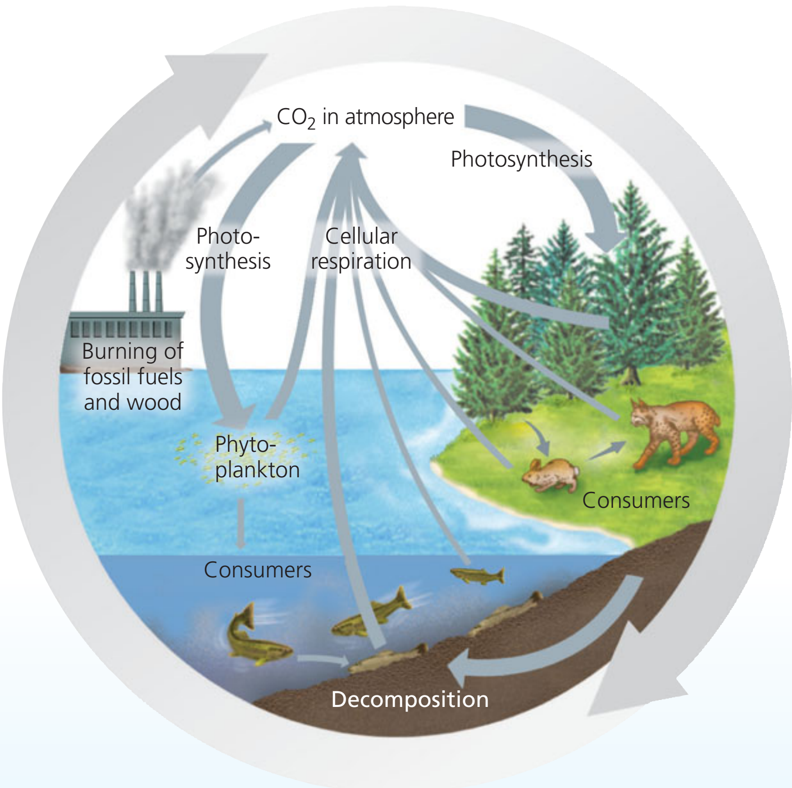
Forms available to life All organisms are capable of exchanging water directly with their environment. Liquid water is the primary physical phase in which water is used, though some organisms can harvest water vapor. Freezing of soil water can limit water availability to terrestrial plants.

Reservoirs The oceans contain 97% of the water in the biosphere. Approximately 2% is bound in glaciers and polar ice caps, and the remaining 1% is in lakes, rivers, and groundwater, with a negligible amount in the atmosphere.

Key processes The main processes driving the water cycle are evaporation of liquid water by solar energy, condensation of water vapor into clouds, and precipitation. Transpiration by terrestrial plants also moves large volumes of water into the atmosphere. Surface and groundwater flow can return water to the oceans, completing the water cycle.



The Carbon Cycle

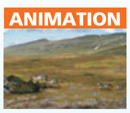


Biological importance Carbon forms the framework of the organic molecules essential to all organisms.

Forms available to life Photosynthetic organisms utilize CO_2 during photosynthesis and convert the carbon to organic forms that are used by consumers, including animals, fungi, and heterotrophic protists and prokaryotes.

Reservoirs The major reservoirs of carbon include fossil fuels, soils, the sediments of aquatic ecosystems, the oceans (dissolved carbon compounds), plant and animal biomass, and the atmosphere (CO_2). The largest reservoir is sedimentary rocks such as limestone; however, this pool turns over very slowly. All organisms are capable of returning carbon directly to their environment in its original form (CO_2) through respiration.

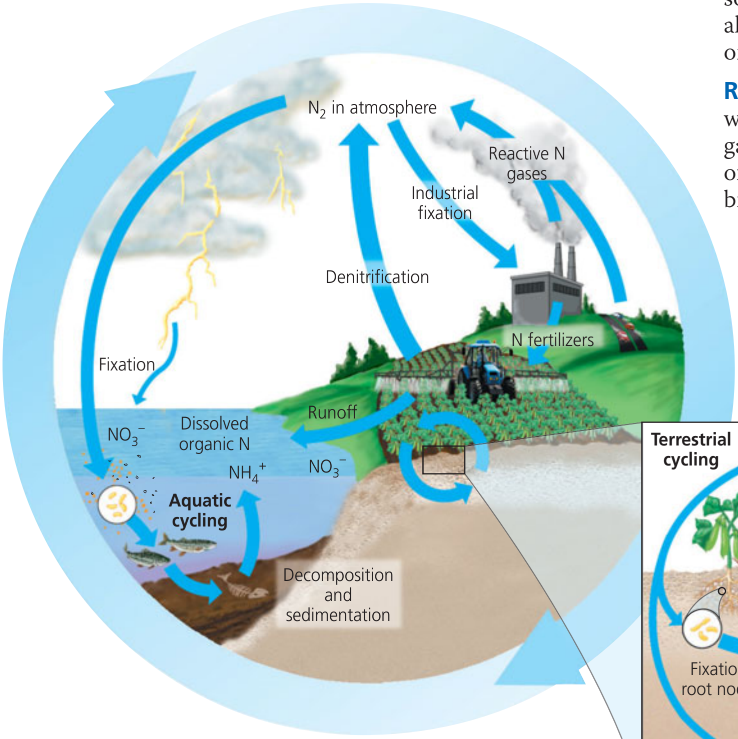
Key processes Photosynthesis by plants and phytoplankton removes substantial amounts of atmospheric CO_2 each year. This quantity is approximately equaled by CO_2 added to the atmosphere through cellular respiration by producers and consumers. The burning of fossil fuels and wood is adding significant amounts of additional CO_2 to the atmosphere. Over geologic time, volcanoes are also a substantial source of CO_2.



BioFlix Visit the Study Area in **MasteringBiology** for the BioFlix® 3-D Animation on The Carbon Cycle.

The Nitrogen Cycle

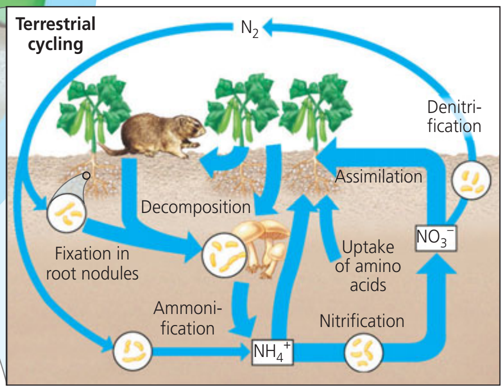
Biological importance Nitrogen is part of amino acids, proteins, and nucleic acids and is often a limiting plant nutrient.



Forms available to life Plants can assimilate (use) two inorganic forms of nitrogen—ammonium (NH_4^+) and nitrate (NO_3^-)—and some organic forms, such as amino acids. Various bacteria can use all of these forms as well as nitrite (NO_2^-). Animals can use only organic forms of nitrogen.

Reservoirs The main reservoir of nitrogen is the atmosphere, which is 78% free nitrogen gas (N_2). The other reservoirs of inorganic and organic nitrogen compounds are soils and the sediments of lakes, rivers, and oceans; surface water and groundwater; and the biomass of living organisms.

Key processes The major pathway for nitrogen to enter an ecosystem is via *nitrogen fixation*, the conversion of N_2 to forms that can be used to synthesize organic nitrogen compounds. Certain bacteria, as well as lightning and volcanic activity, fix nitrogen naturally. Nitrogen inputs from human activities now outpace natural inputs on land. Two major contributors are industrially produced fertilizers and legume crops that fix nitrogen via bacteria in their root nodules. Other bacteria in soil convert nitrogen to different forms. Some bacteria carry out denitrification, the reduction of nitrate to nitrogen gases. Human activities also release large quantities of reactive nitrogen gases, such as nitrogen oxides, to the atmosphere.



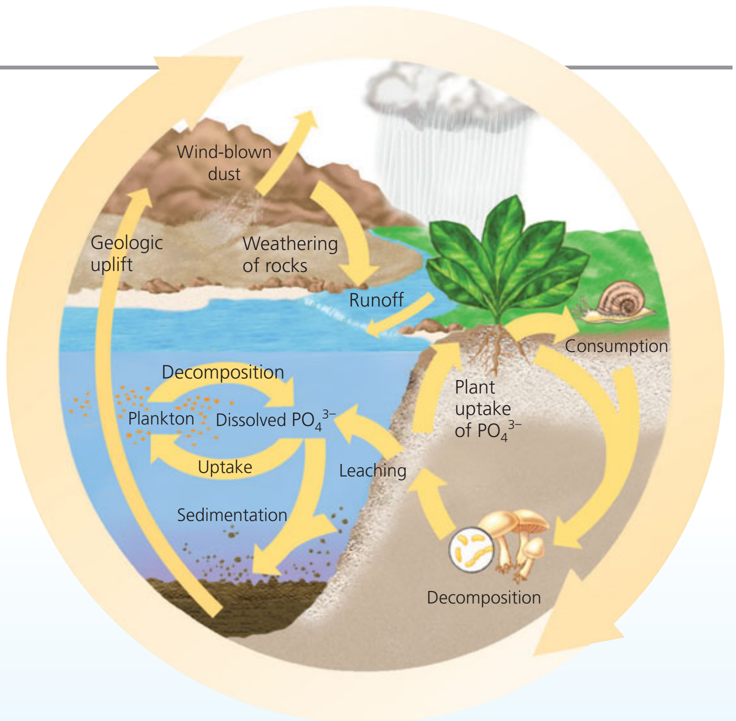
The Phosphorus Cycle

Biological importance Organisms require phosphorus as a major constituent of nucleic acids, phospholipids, and ATP and other energy-storing molecules and as a mineral constituent of bones and teeth.

Forms available to life The most biologically important inorganic form of phosphorus is phosphate (PO_4^{3-}), which plants absorb and use in the synthesis of organic compounds.

Reservoirs The largest accumulations of phosphorus are in sedimentary rocks of marine origin. There are also large quantities of phosphorus in soil, in the oceans (in dissolved form), and in organisms. Because soil particles bind PO_4^{3-}, the recycling of phosphorus tends to be quite localized in ecosystems.

Key processes Weathering of rocks gradually adds PO_4^{3-} to soil; some leaches into groundwater and surface water and may eventually reach the sea. Phosphate taken up by producers and incorporated into biological molecules may be eaten by consumers. Phosphate is returned to soil or water by either decomposition of biomass or excretion by consumers. Because there are no significant phosphorus-containing gases, only relatively small amounts of phosphorus move through the atmosphere, usually in the forms of dust and sea spray.



cycle, consider which steps are driven primarily by biological processes. For the carbon cycle, for instance, plants, animals, and other organisms control most of the key steps, including photosynthesis and decomposition. For the water cycle, however, purely physical processes control many key steps, such as evaporation from the oceans.

How have ecologists worked out the details of chemical cycling in various ecosystems? One common method is to follow the movement of naturally occurring, nonradioactive isotopes through the biotic and abiotic components of an ecosystem. Another method involves adding tiny amounts of radioactive isotopes of specific elements and tracing their progress. Scientists have also been able to make use of the radioactive carbon (^{14}C) released into the atmosphere during atom bomb testing in the 1950s and early 1960s. Scientists use this "spike" of ^{14}C to trace where and how quickly carbon flows into ecosystem components, including plants, soils, and ocean water.

Case Study: Nutrient Cycling in the Hubbard Brook Experimental Forest

Since 1963, ecologists Herbert Bormann, Gene Likens, and their colleagues have been studying nutrient cycling at the Hubbard Brook Experimental Forest in the White Mountains of New Hampshire. Their research site is a deciduous forest that grows in six small valleys, each drained by a single creek. Impenetrable bedrock underlies the soil of the forest.

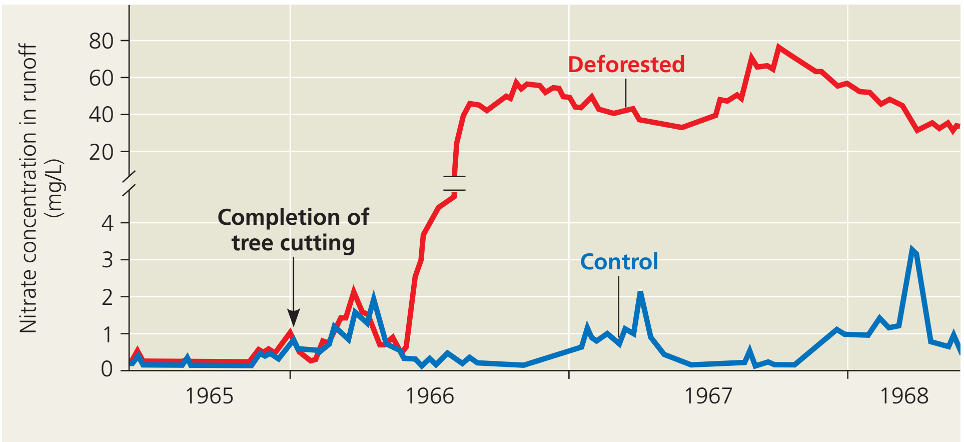
The research team first determined the mineral budget for each of six valleys by measuring the input and outflow of several key nutrients. They collected rainfall at several sites to measure the amount of water and dissolved minerals added to the ecosystem. To monitor the loss of water and minerals, they constructed a small concrete dam with a V-shaped spillway across the creek at the bottom of each valley (**Figure 42.14a**). They found that about 60% of the water added to the ecosystem as rainfall and snow exits through the stream, and the remaining 40% is lost by evapotranspiration.

Preliminary studies confirmed that internal cycling conserved most of the mineral nutrients in the system. For example, only about 0.3% more calcium (Ca^{2+}) leaves a valley via its creek than is added by rainwater, and this small net loss is probably replaced by chemical decomposition of the bedrock. During most years, the forest even registers small net gains of a few mineral nutrients, including nitrogen.

Experimental deforestation of a watershed dramatically increased the flow of water and minerals leaving the watershed (**Figure 42.14b**). Over three years, water runoff from the newly deforested watershed was 30–40% greater than in a control watershed, apparently because there were no plants to absorb and transpire water from the soil. Most remarkable was the loss of nitrate, whose concentration in the creek increased 60-fold, reaching levels considered unsafe for drinking water (**Figure 42.14c**). The Hubbard Brook deforestation study showed that the amount of nutrients leaving an intact forest ecosystem is controlled mainly by the plants. Retaining

(a) Concrete dams and weirs built across streams at the bottom of watersheds enabled researchers to monitor the outflow of water and nutrients from the ecosystem.

(b) One watershed was clear-cut to study the effects of the loss of vegetation on drainage and nutrient cycling. All of the original plant material was left in place to decompose.



(c) The concentration of nitrate in runoff from the deforested watershed was 60 times greater than in a control (unlogged) watershed.

▲ **Figure 42.14 Nutrient cycling in the Hubbard Brook Experimental Forest: an example of long-term ecological research.**

MB A related Experimental Inquiry Tutorial can be assigned in MasteringBiology.

nutrients in ecosystems helps to maintain the productivity of the systems and, in some cases, to avoid problems caused by excess nutrient runoff (see Figure 42.7).

CONCEPT CHECK 42.4

1. **DRAW IT** For each of the four biogeochemical cycles detailed in Figure 42.12, draw a simple diagram that shows one possible path for an atom of that chemical from abiotic to biotic reservoirs and back.
2. Why does deforestation of a watershed increase the concentration of nitrates in streams draining the watershed?
3. **WHAT IF?** Why is nutrient availability in a tropical rain forest particularly vulnerable to logging?

For suggested answers, see Appendix A.

CONCEPT 42.5

Restoration ecologists help return degraded ecosystems to a more natural state

Ecosystems can recover naturally from most disturbances (including the experimental deforestation at Hubbard Brook) through the stages of ecological succession (see Concept 41.3). Sometimes that recovery takes centuries, though, particularly when human activities have degraded the environment. Tropical areas that are cleared for farming may quickly become unproductive because of nutrient losses. Mining activities may last for several decades, and the lands are often abandoned in a degraded state. Ecosystems can also be damaged by salts that build up in soils from irrigation and by toxic chemicals or oil spills. Biologists increasingly are called on to help restore and repair damaged ecosystems.

One of the basic assumptions of restoration ecology is that environmental damage is at least partly reversible. This optimistic view must be balanced by a second assumption—that ecosystems are not infinitely resilient. Restoration ecologists therefore work to identify and manipulate the processes that most limit recovery of ecosystems from disturbances. Where disturbance is so severe that restoring all of a habitat is impractical, ecologists try to reclaim as much of a habitat or ecological process as possible, within the limits of the time and money available to them.

In extreme cases, the physical structure of an ecosystem may need to be restored before biological restoration can occur. If a stream was straightened to channel water quickly through a suburb, restoration ecologists may reconstruct a meandering channel to slow down the flow of water eroding the stream bank. To restore an open-pit mine, engineers may first grade the site with heavy equipment to reestablish a gentle slope, spreading topsoil when the slope is in place **(Figure 42.15)**.

Once physical reconstruction of the ecosystem is complete—or when it is not needed—biological restoration is the next step. Two key strategies in biological restoration are bioremediation and biological augmentation.

Bioremediation

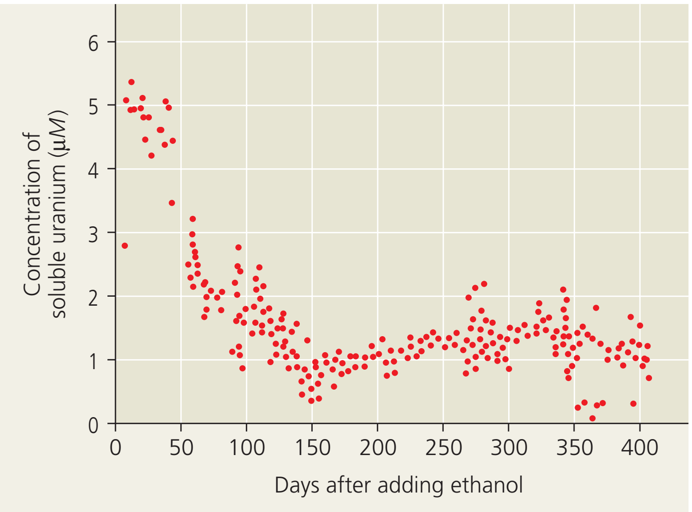
Using organisms—usually prokaryotes, fungi, or plants—to detoxify polluted ecosystems is known as **bioremediation**. Some plants and lichens adapted to soils containing heavy metals can accumulate high concentrations of toxic metals such as zinc, lead, and cadmium in their tissues. Restoration ecologists can introduce such species to sites polluted by mining and other human activities and then harvest these organisms to remove the metals from the ecosystem. For instance, researchers in the United Kingdom have discovered a lichen species that grows on soil polluted with uranium dust left over from mining. The lichen concentrates uranium in a dark pigment, making it useful as a biological monitor and potentially as a remediator.

(a) In 1991, before restoration **(b)** In 2000, near the completion of restoration

▲ **Figure 42.15 A gravel and clay mine site in New Jersey before and after restoration.**

Ecologists already use the abilities of many prokaryotes to carry out bioremediation of soils and water. Scientists have sequenced the genomes of at least ten prokaryotic species specifically for their bioremediation potential. One of the species, the bacterium *Shewanella oneidensis*, appears particularly promising. It can metabolize a dozen or more elements under aerobic and anaerobic conditions. In doing so, it converts soluble forms of uranium, chromium, and nitrogen to insoluble forms that are less likely to leach into streams or groundwater. Researchers at Oak Ridge National Laboratory, in Tennessee, stimulated the growth of *Shewanella* and other uranium-reducing bacteria by adding ethanol to groundwater contaminated with uranium; the bacteria can use ethanol as an energy source. In just five months, the concentration of soluble uranium in the ecosystem dropped by 80% **(Figure 42.16)**.

(a) Wastes containing uranium were dumped in these four unlined pits for more than 30 years, contaminating soils and groundwater.



(b) After ethanol was added, microbial activity decreased the concentration of soluble uranium in groundwater near the pits.

▲ **Figure 42.16 Bioremediation of groundwater contaminated with uranium at Oak Ridge National Laboratory, Tennessee.**

Biological Augmentation

In contrast to bioremediation, which is a strategy for removing harmful substances from an ecosystem, **biological augmentation** uses organisms to *add* essential materials to a degraded ecosystem. To augment ecosystem processes, restoration ecologists need to determine which factors, such as chemical nutrients, have been lost from a system and are limiting its recovery.

Encouraging the growth of plants that thrive in nutrient-poor soils often speeds up succession and ecosystem recovery. In alpine ecosystems of the western United States, nitrogen-fixing plants such as lupines are often planted to raise nitrogen concentrations in soils disturbed by mining and other activities. Once these nitrogen-fixing plants become established, other native species are better able to obtain enough soil nitrogen to survive. In other systems where the soil has been severely disturbed or where topsoil is missing entirely, plant roots may lack the mycorrhizal symbionts that help them meet their nutritional needs (see Chapter 26). Ecologists restoring a tallgrass prairie in Minnesota recognized this limitation and enhanced the recovery of native species by adding mycorrhizal symbionts to the soil they seeded.

Restoring the physical structure and plant community of an ecosystem does not necessarily ensure that animal species will recolonize a site and persist there. Because animals provide critical ecosystem services, including pollination and seed dispersal, restoration ecologists sometimes help wildlife reach and use restored ecosystems. They might release animals at a site or establish habitat corridors that connect a restored site to other places where the animals are found. They sometimes establish artificial perches for birds or dig burrows for other animals to use. Such efforts can improve the biodiversity of restored ecosystems and help the community persist.

Restoration Projects Worldwide

Because restoration ecology is a relatively new discipline and because ecosystems are complex, many restoration ecologists advocate adaptive management: experimenting with several promising types of management to learn what works best.

The long-term objective of restoration is to return an ecosystem as much as possible to its predisturbance state. **Figure 42.17** explores four ambitious and successful restoration projects. The great number of such projects around the world and the dedication of the people engaged in them suggest that restoration ecology will continue to grow as a discipline for many years.

CONCEPT CHECK 42.5

1. Identify the main goal of restoration ecology.
2. How do bioremediation and biological augmentation differ?
3. **WHAT IF?** In what way is the Kissimmee River project a more complete ecological restoration than the Maungatautari project (see Figure 42.17)?

For suggested answers, see Appendix A.

▼ Figure 42.17 **Exploring Restoration Ecology Worldwide**

The examples highlighted on this page are just a few of the many restoration ecology projects taking place around the world.

► Kissimmee River, Florida

The Kissimmee River was converted from a meandering river to a 90-km canal, threatening many fish and wetland bird populations. Kissimmee River restoration has filled 12 km of drainage canal and reestablished 24 km of the original 167 km of natural river channel. Pictured here is a section of the Kissimmee canal that has been plugged (wide, light strip on the right side of the photo), diverting flow into remnant river channels (center of the photo). The project will also restore natural flow patterns, which will foster self-sustaining populations of wetland birds and fishes.

◄ Succulent Karoo, South Africa

In this desert region of southern Africa, as in many arid regions, overgrazing by livestock has damaged vast areas. Private landowners and government agencies in South Africa are restoring large areas of this unique region, revegetating the land and employing more sustainable resource management. The photo shows a small sample of the exceptional plant diversity of the Succulent Karoo; its 5,000 plant species include the highest diversity of succulent plants in the world.

► Maungatautari, New Zealand

Weasels, rats, pigs, and other introduced species pose a serious threat to New Zealand's native plants and animals, including kiwis, a group of flightless, ground-dwelling bird species. The goal of the Maungatautari restoration project is to exclude all exotic mammals from a 3,400-ha reserve located on a forested volcanic cone. A specialized fence around the reserve eliminates the need to continue setting traps and using poisons that can harm native wildlife. In 2006, a pair of critically endangered takahe (a species of flightless rail) were released into the reserve in hopes of reestablishing a breeding population of this colorful bird on New Zealand's North Island.

◄ Coastal Japan

Seaweed and seagrass beds are important nursery grounds for a wide variety of fishes and shellfish. Once extensive but now reduced by development, these beds are being restored in the coastal areas of Japan. Techniques include constructing suitable seafloor habitat, transplanting from natural beds using artificial substrates, and hand seeding (shown in this photograph).

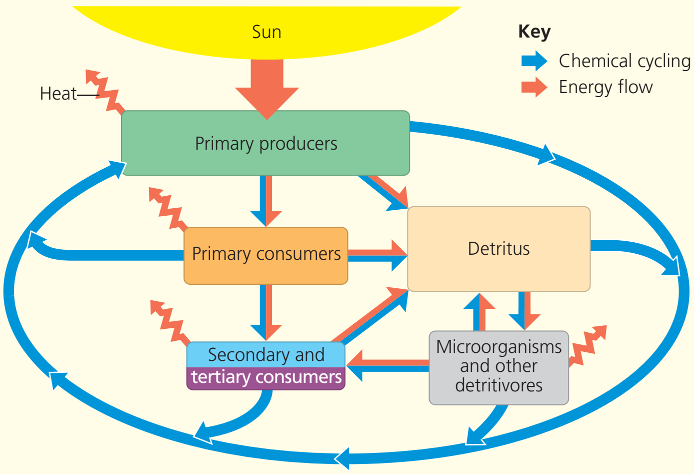
42 Chapter Review

SUMMARY OF KEY CONCEPTS

CONCEPT 42.1

Physical laws govern energy flow and chemical cycling in ecosystems (pp. 865–866)

- An **ecosystem** consists of all the organisms in a community and the abiotic factors with which they interact. The laws of physics and chemistry apply to ecosystems, particularly for the conservation of energy. Energy is conserved but degraded to heat during ecosystem processes.
- Based on the **law of conservation of mass**, ecologists study how much of a chemical element enters and leaves an ecosystem and cycles within it. Inputs and outputs are generally small compared to recycled amounts, but their balance determines whether the ecosystem gains or loses an element over time.



? *Based on the second law of thermodynamics, would you expect the typical biomass of primary producers in an ecosystem to be greater than or less than the biomass of secondary producers in the same ecosystem? Explain your reasoning.*

CONCEPT 42.2

Energy and other limiting factors control primary production in ecosystems (pp. 866–870)

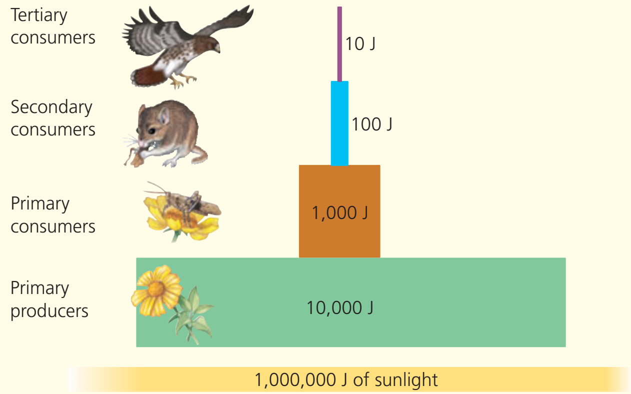
- **Primary production** sets the spending limit for the global energy budget. **Gross primary production** is the total energy assimilated by an ecosystem in a given period. **Net primary production**, the energy accumulated in autotroph biomass, equals gross primary production minus the energy used by the primary producers for respiration. **Net ecosystem production** is the total biomass accumulation of an ecosystem, defined as the difference between gross primary production and total ecosystem respiration.
- In aquatic ecosystems, light and nutrients limit primary production. In terrestrial ecosystems, climatic factors such as temperature and moisture affect primary production on a large geographic scale, but a soil nutrient is often the limiting factor in primary production locally.

? *What additional variable do you need to know the value of in order to estimate NEP from NPP? Why might measuring this variable be difficult, for instance, in a sample of ocean water?*

CONCEPT 42.3

Energy transfer between trophic levels is typically only 10% efficient (pp. 870–872)

- The amount of energy available to each trophic level is determined by the net primary production and the **production efficiency**, the efficiency with which food energy is converted to biomass at each link in the food chain.
- The percentage of energy transferred from one trophic level to the next, called **trophic efficiency**, is typically 10%. Pyramids of net production and biomass reflect low trophic efficiency.



? *Why would runners have a lower production efficiency when running a long-distance race than when they are sedentary?*

CONCEPT 42.4

Biological and geochemical processes cycle nutrients and water in ecosystems (pp. 872–877)

- Water moves in a global cycle driven by solar energy. The carbon cycle primarily reflects the reciprocal processes of photosynthesis and cellular respiration.
- The proportion of a nutrient in a particular form and its cycling in that form vary among ecosystems, largely because of differences in the rate of decomposition.
- Nutrient cycling is strongly regulated by vegetation. The Hubbard Brook case study showed that logging increases water runoff and can cause large losses of minerals.

? *If decomposers usually grow faster and decompose material more quickly in warmer ecosystems, why is decomposition in hot deserts so slow?*

CONCEPT 42.5

Restoration ecologists help return degraded ecosystems to a more natural state (pp. 877–879)

- Restoration ecologists harness organisms to detoxify polluted ecosystems through the process of **bioremediation**.
- In **biological augmentation**, ecologists use organisms to add essential materials to ecosystems.

? *In preparing a site for surface mining and later restoration, what would be the advantage of removing the shallow topsoil first and setting it aside separately from the deeper soil, rather than removing all soil at once and mixing it in a single pile?*

TEST YOUR UNDERSTANDING

Level 1: Knowledge/Comprehension

1. Which of the following organisms is *incorrectly* paired with its trophic level?
- **a.** cyanobacterium—primary producer
- **b.** grasshopper—primary consumer
- **c.** zooplankton—primary producer
- **d.** eagle—tertiary consumer
- **e.** fungus—detritivore

2. Which of these ecosystems has the *lowest* net primary production per square meter?
- **a.** a salt marsh
- **b.** an open ocean
- **c.** a coral reef
- **d.** a grassland
- **e.** a tropical rain forest

3. The discipline that applies ecological principles to returning degraded ecosystems to a more natural state is known as
- **a.** population viability analysis.
- **b.** landscape ecology.
- **c.** conservation ecology.
- **d.** restoration ecology.
- **e.** resource conservation.

Level 2: Application/Analysis

4. Nitrifying bacteria participate in the nitrogen cycle mainly by
- **a.** converting nitrogen gas to ammonia.
- **b.** releasing ammonium from organic compounds, thus returning it to the soil.
- **c.** converting ammonia to nitrogen gas, which returns to the atmosphere.
- **d.** converting ammonium to nitrate, which plants absorb.
- **e.** incorporating nitrogen into amino acids and organic compounds.

5. Which of the following has the greatest effect on the rate of chemical cycling in an ecosystem?
- **a.** the ecosystem's rate of primary production
- **b.** the production efficiency of the ecosystem's consumers
- **c.** the rate of decomposition in the ecosystem
- **d.** the trophic efficiency of the ecosystem
- **e.** the location of the nutrient reservoirs in the ecosystem

6. The Hubbard Brook watershed deforestation experiment yielded all of the following results *except*:
- **a.** Most minerals were recycled within a forest ecosystem.
- **b.** The flow of minerals out of a natural watershed was offset by minerals flowing in.
- **c.** Deforestation increased water runoff.
- **d.** The nitrate concentration in waters draining the deforested area became dangerously high.
- **e.** Calcium levels remained high in the soil of deforested areas.

7. Which of the following would be considered an example of bioremediation?
- **a.** adding nitrogen-fixing microorganisms to a degraded ecosystem to increase nitrogen availability
- **b.** using a bulldozer to regrade a strip mine
- **c.** dredging a river bottom to remove contaminated sediments
- **d.** reconfiguring the channel of a river
- **e.** adding seeds of a chromium-accumulating plant to soil contaminated by chromium

8. If you applied a fungicide to a cornfield, what would you expect to happen to the rate of decomposition and net ecosystem production (NEP)?
- **a.** Both decomposition rate and NEP would decrease.
- **b.** Both decomposition rate and NEP would increase.
- **c.** Neither would change.
- **d.** Decomposition rate would increase and NEP would decrease.
- **e.** Decomposition rate would decrease and NEP would increase.

Level 3: Synthesis/Evaluation

9. **DRAW IT** Draw a simplified global water cycle showing ocean, land, atmosphere, and runoff from the land to the ocean. Add these annual water fluxes to your drawing: ocean evaporation, 425 km^3; ocean evaporation that returns to the ocean as precipitation, 385 km^3; ocean evaporation that falls as precipitation on land, 40 km^3; evapotranspiration from plants and soil that falls as precipitation on land, 70 km^3; runoff to the oceans, 40 km^3. Based on these global numbers, how much precipitation falls on land in a typical year?

10. **SCIENTIFIC INQUIRY**
Using two neighboring ponds in a forest as your study site, design a controlled experiment to measure the effect of falling leaves on net primary production in a pond.

11. **FOCUS ON EVOLUTION**
Some biologists have suggested that ecosystems are emergent, "living" systems capable of evolving. One manifestation of this idea is environmentalist James Lovelock's Gaia hypothesis, which views Earth itself as a living, homeostatic entity—a kind of superorganism. If ecosystems are capable of evolving, would this be a form of Darwinian evolution? Why or why not?

12. **FOCUS ON ENERGY AND MATTER**
As described in Concept 42.4, decomposition typically occurs quickly in moist tropical forests. However, waterlogging in the soil of some moist tropical forests results over time in a buildup of organic matter called "peat." In a short essay (100–150 words), discuss the relationship of net primary production, net ecosystem production, and decomposition for such an ecosystem. Are NPP and NEP likely to be positive? What do you think would happen to NEP if a landowner drained the water from a tropical peatland, exposing the organic matter to air?

For selected answers, see Appendix A.

43 Global Ecology and Conservation Biology

KEY CONCEPTS

43.1 Human activities threaten Earth's biodiversity

43.2 Population conservation focuses on population size, genetic diversity, and critical habitat

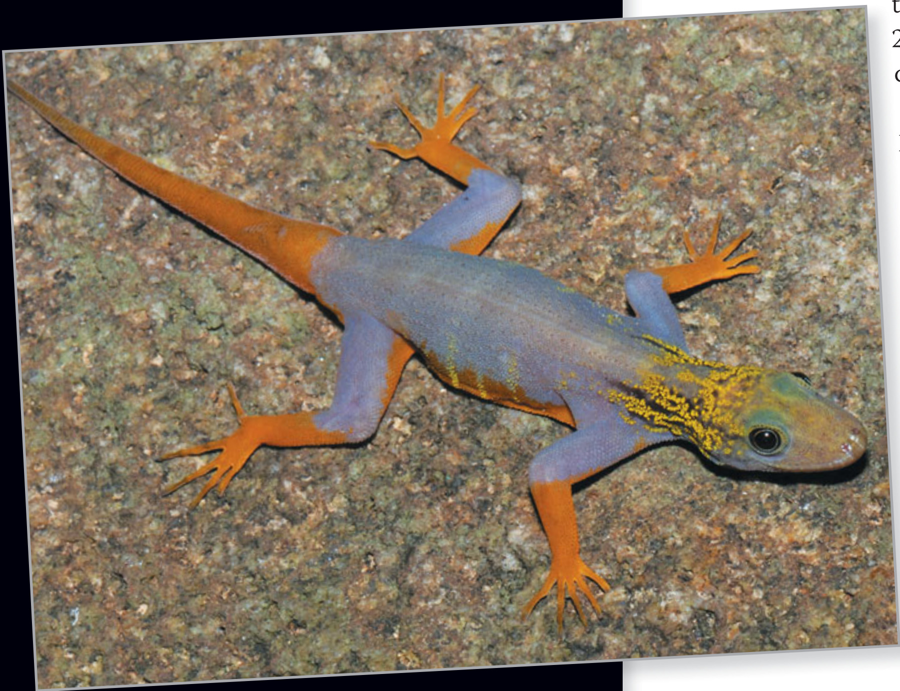
43.3 Landscape and regional conservation help sustain biodiversity

43.4 Earth is changing rapidly as a result of human actions

43.5 The human population is no longer growing exponentially but is still increasing rapidly

43.6 Sustainable development can improve human lives while conserving biodiversity

▼ **Figure 43.1** What will be the fate of this newly described lizard species?



OVERVIEW

Psychedelic Treasure

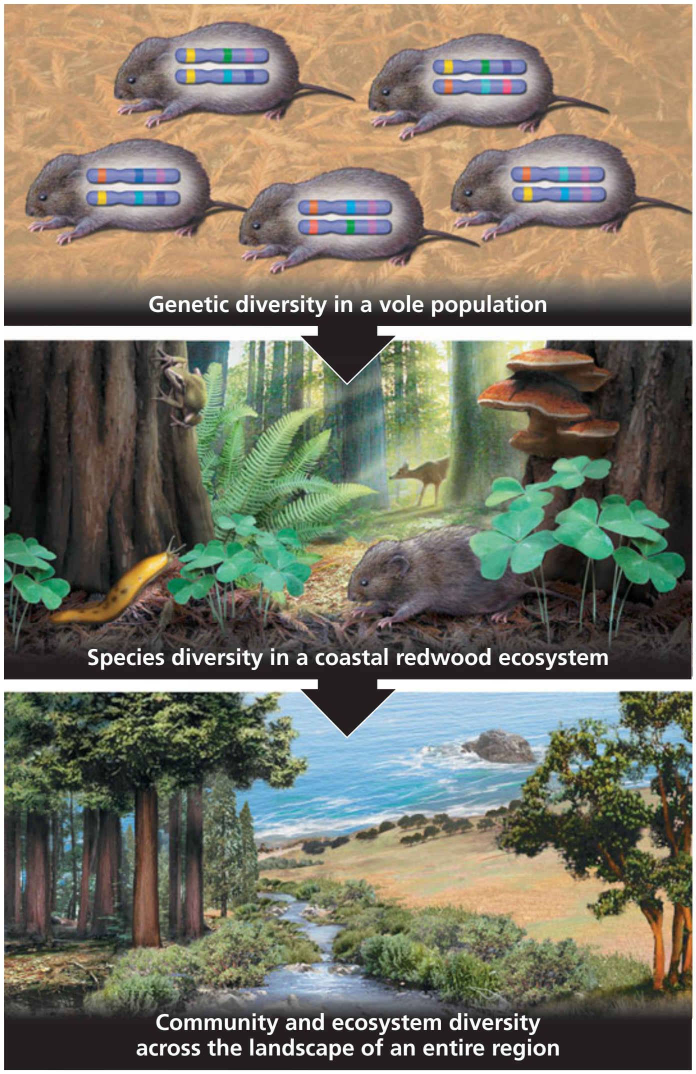
Scurrying across a rocky outcrop, a lizard stops abruptly in a patch of sunlight. A conservation biologist senses the motion and turns to find a gecko splashed with rainbow colors, its bright orange legs and tail blending into a striking blue body, its head splotched with yellow and green. The psychedelic rock gecko (*Cnemaspis psychedelica*) was discovered in 2010 during an expedition to the Greater Mekong region of southeast Asia (**Figure 43.1**). Its known habitat is restricted to Hon Khoai, an island occupying just 8 km^2 (3 square miles) in southern Vietnam. Other new species found during the same series of expeditions include the Elvis monkey, which sports a hairdo like that of a certain legendary musician. Between 2000 and 2010, biologists identified more than a thousand new species in the Greater Mekong region alone.

To date, scientists have described and named about 1.8 million species of organisms. Some biologists think that about 10 million more species currently exist; others estimate the number to be as high as 100 million. The greatest concentrations of species are found in the tropics. Unfortunately, tropical forests are being cleared at an alarming rate to support a burgeoning human population. In Vietnam, rates of deforestation are among the very highest in the world (**Figure 43.2**). What will become of the psychedelic rock gecko and other newly discovered species if such activities continue unchecked?

Throughout the biosphere, human activities are altering trophic structures, energy flow, chemical cycling, and natural disturbance—ecosystem processes on which we and all other species depend (see Chapter 42). We have physically altered nearly half of Earth's land surface, and we use over half of all accessible surface fresh water. In the oceans, stocks of most major fisheries are shrinking because of overharvesting. By some estimates, we may be pushing more species toward extinction than the large asteroid that triggered the mass extinctions at the close of the Cretaceous period 65.5 million years ago (see Figure 23.10).

In this chapter, we apply a global perspective to the changes happening across Earth, focusing on a discipline that seeks to preserve life: **Conservation biology** integrates ecology, evolutionary biology, molecular biology, genetics,

▲ **Figure 43.2 Tropical deforestation in Vietnam.**



▲ **Figure 43.3 Three levels of biodiversity.** The oversized chromosomes in the top diagram symbolize the genetic variation within the population.

and physiology to conserve biological diversity at all levels. Efforts to sustain ecosystem processes and stem the loss of biodiversity also connect the life sciences with the social sciences, economics, and humanities.

We'll begin by taking a closer look at the biodiversity crisis and examining some of the conservation strategies being adopted to slow the rate of species loss. We'll also examine how human activities are altering the environment through climate change and other global processes, and we'll investigate the link between these alterations and the growing human population. Finally, we'll consider how decisions about long-term conservation priorities could affect life on Earth.

CONCEPT 43.1

Human activities threaten Earth's biodiversity

Extinction is a natural phenomenon that has been occurring since life first evolved; it is the high *rate* of extinction that is responsible for today's biodiversity crisis (see Chapter 23). Because we can only estimate the number of species currently existing, we cannot determine the exact rate of species loss. However, we do know that human activities threaten Earth's biodiversity at all levels.

Three Levels of Biodiversity

Biodiversity—short for biological diversity—can be considered at three main levels: genetic diversity, species diversity, and ecosystem diversity **(Figure 43.3)**.

Genetic Diversity

Genetic diversity comprises not only the individual genetic variation *within* a population, but also the genetic variation *between* populations that is often associated with adaptations to local conditions (see Chapter 21). If one population becomes extinct, then a species may have lost some of the genetic diversity that makes microevolution possible. This erosion of genetic diversity in turn reduces the adaptive potential of the species.

Species Diversity

Public awareness of the biodiversity crisis centers on species diversity—the variety of species in an ecosystem or across the biosphere (see Chapter 41). As more species are lost to extinction, species diversity decreases. The U.S. Endangered Species Act defines an **endangered species** as one that is "in danger of extinction throughout all or a significant portion of its range." **Threatened species** are those considered likely to become endangered in the near future. The following are just a few statistics that illustrate the problem of species loss:

- According to the International Union for Conservation of Nature and Natural Resources (IUCN), 12% of the 10,000 known species of birds and 21% of the 5,500 known species of mammals are threatened.

▲ **Figure 43.4 A hundred heartbeats from extinction.** These are two members of what E. O. Wilson calls the Hundred Heartbeat Club, species with fewer than 100 individuals remaining on Earth. The Yangtze River dolphin was even thought to be extinct, but a few individuals were reportedly sighted in 2007.

? *To document that a species has actually become extinct, what factors would you need to consider?*

- A survey by the Center for Plant Conservation showed that of the nearly 20,000 known plant species in the United States, 200 have become extinct since such records have been kept, and 730 are endangered or threatened.
- In North America, at least 123 freshwater animal species have become extinct since 1900, and hundreds more species are threatened. The extinction rate for North American freshwater fauna is about five times as high as that for terrestrial animals.

Extinction of species may also be local; for example, a species may be lost in one river system but survive in an adjacent one. Global extinction of a species means that it is lost from *all* the ecosystems in which it lived, leaving them permanently impoverished **(Figure 43.4)**.

Ecosystem Diversity

The variety of the biosphere's ecosystems is a third level of biological diversity. Because of the many interactions between populations of different species in an ecosystem, the local extinction of one species can have a negative impact on other species in the ecosystem (see Figure 41.15). For instance, bats called "flying foxes" are important pollinators and seed dispersers in the Pacific Islands, where they are increasingly hunted as a luxury food **(Figure 43.5)**. Conservation biologists fear that the extinction of flying foxes would also harm the native plants of the Samoan Islands, where four-fifths of the tree species depend on flying foxes for pollination or seed dispersal.

▲ **Figure 43.5 The endangered Marianas "flying fox" bat (*Pteropus mariannus*), an important pollinator.**

Some ecosystems have already been heavily affected by humans, and others are being altered at a rapid pace. Since European colonization, more than half of the wetlands in the contiguous United States have been drained and converted to agricultural and other uses. In California, Arizona, and New Mexico, roughly 90% of native riparian (streamside) communities have been affected by overgrazing, flood control, water diversions, lowering of water tables, and invasion by non-native plants.

Biodiversity and Human Welfare

Why should we care about the loss of biodiversity? One reason is what Harvard biologist E. O. Wilson calls *biophilia*, our sense of connection to nature and all life. The belief that other species are entitled to life is a pervasive theme of many religions and the basis of a moral argument that we should protect biodiversity. There is also a concern for future human generations. Paraphrasing an old proverb, G. H. Brundtland, a former prime minister of Norway, said: "We must consider our planet to be on loan from our children, rather than being a gift from our ancestors." In addition to such philosophical and moral justifications, species and genetic diversity bring us many practical benefits.

Benefits of Species and Genetic Diversity

Many species that are threatened could potentially provide medicines, food, and fibers for human use, making biodiversity a crucial natural resource. Products from aspirin to antibiotics were originally derived from natural sources. In food production, if we lose wild populations of plants closely related to agricultural species, we lose genetic resources that could be used to improve crop qualities, such as disease resistance. For instance, plant breeders responded to devastating outbreaks of the grassy stunt virus in rice (*Oryza sativa*) by screening 7,000 populations of this species and its close relatives for resistance to the virus. One population of a single relative, Indian rice (*Oryza nivara*), was found to be resistant to the virus, and scientists succeeded in breeding the resistance trait into commercial rice varieties. Today, the original disease-resistant population has apparently become extinct in the wild.

In the United States, about 25% of the prescriptions dispensed from pharmacies contain substances originally derived from plants. In the 1970s, researchers discovered that the rosy periwinkle (*Catharanthus roseus*), which grows on the island of Madagascar, off the coast of Africa, contains alkaloids that inhibit cancer cell growth. This discovery led to treatments for two deadly forms of cancer, Hodgkin's lymphoma and childhood leukemia, resulting in remission in most cases.

Rosy periwinkle

Each loss of a species means the loss of unique genes, some of which may code for enormously useful proteins. The enzyme Taq polymerase was first extracted from a bacterium, *Thermus aquaticus*, found in hot springs at Yellowstone National Park. This enzyme is essential for the polymerase chain reaction (PCR) because it is stable at the high temperatures required for automated PCR (see Figure 13.25). However, because millions of species may become extinct before we discover them, we stand to lose the valuable genetic potential held in their unique libraries of genes.

Ecosystem Services

The benefits that individual species provide to humans are substantial, but saving individual species is only part of the reason for preserving ecosystems. We humans evolved in Earth's ecosystems, and we rely on these systems and their inhabitants for our survival. **Ecosystem services** encompass all the processes through which natural ecosystems help sustain human life. Ecosystems purify our air and water. They detoxify and decompose our wastes and reduce the impacts of extreme weather and flooding. The organisms in ecosystems pollinate our crops, control pests, and create and preserve our soils. Moreover, these diverse services are provided for free.

Perhaps because we don't attach a monetary value to the services of natural ecosystems, we generally undervalue them. In 1997, ecologist Robert Costanza and his colleagues estimated the value of Earth's ecosystem services at $33 trillion per year, nearly twice the gross national product of all the countries on Earth at the time ($18 trillion). It may be more realistic to do the accounting on a smaller scale. In 1996, New York City invested more than $1 billion to buy land and restore habitat in the Catskill Mountains, the source of much of the city's fresh water. This investment was spurred by increasing pollution of the water by sewage, pesticides, and fertilizers. By harnessing ecosystem services to purify its water naturally, the city saved $8 billion it would have otherwise spent to build a new water treatment plant and $300 million a year to run the plant.

There is growing evidence that the functioning of ecosystems, and hence their capacity to perform services, is linked to biodiversity. As human activities reduce biodiversity, we are reducing the capacity of the planet's ecosystems to perform processes critical to our own survival.

Threats to Biodiversity

Many different human activities threaten biodiversity on local, regional, and global scales. The threats posed by these activities are of four major types: habitat loss, introduced species, overharvesting, and global change.

Habitat Loss

Human alteration of habitat is the single greatest threat to biodiversity throughout the biosphere. Habitat loss has been brought about by agriculture, urban development, forestry, mining, and pollution. As discussed later in this chapter, global climate change is already altering habitats today and will have an even larger effect later this century. When no alternative habitat is available or a species is unable to move, habitat loss may mean extinction. The IUCN implicates destruction of physical habitat for 73% of the species that have become extinct, endangered, vulnerable, or rare in the last few hundred years.

Habitat loss and fragmentation may occur over large regions. Approximately 98% of the tropical dry forests of Central America and Mexico have been cut down. The clearing of tropical rain forest in the state of Veracruz, Mexico, mostly for cattle ranching, has resulted in the loss of more than 90% of the original forest, leaving relatively small, isolated patches of forest. Other natural habitats have also been fragmented by human activities **(Figure 43.6)**.

▲ **Figure 43.6 Habitat fragmentation in the foothills of Los Angeles.** Development in the valleys may confine the organisms that inhabit the narrow strips of hillside.

In almost all cases, habitat fragmentation leads to species loss because the smaller populations in habitat fragments have a higher probability of local extinction. Prairie covered about 800,000 hectares (ha) of southern Wisconsin when Europeans first arrived in North America but occupies less than 800 ha today; most of the original prairie in this area is now used to grow crops. Plant diversity surveys of 54 Wisconsin prairie remnants conducted in 1948–1954 and repeated in 1987–1988 showed that the remnants lost between 8% and 60% of their plant species in the time between the two surveys.

Habitat loss is also a major threat to aquatic biodiversity. About 70% of coral reefs, among Earth's most species-rich aquatic communities, have been damaged by human activities. At the current rate of destruction, 40–50% of the reefs, home to one-third of marine fish species, could disappear in the next 30 to 40 years. Freshwater habitats are also being lost, often as a result of the dams, reservoirs, channel modification, and flow regulation now affecting most of the world's rivers. For example, the more than 30 dams and locks built along the Mobile River basin in the southeastern United States changed river depth and flow. While providing the benefits of hydroelectric power and increased ship traffic, these dams and locks also helped drive more than 40 species of mussels and snails to extinction.

Introduced Species

Introduced species, also called exotic species, are those that humans move intentionally or accidentally from the species' native locations to new geographic regions. Human travel by ship and airplane has accelerated the transplant of species. Free from the predators, parasites, and pathogens that limit their populations in their native habitats, such transplanted species may spread rapidly through a new region.

Some introduced species disrupt their new community, often by preying on native organisms or outcompeting them for resources. The brown tree snake was accidentally introduced to the island of Guam from other parts of the South Pacific after World War II: It was a "stowaway" in military cargo. Since then, 12 species of birds and 6 species of lizards that the snakes ate have become extinct on Guam, which had no native snakes. The devastating zebra mussel, a filter-feeding mollusc, was introduced into the Great Lakes of North America in 1988, most likely in the ballast water of ships arriving from Europe. Zebra mussels form dense colonies and have disrupted freshwater ecosystems, threatening native aquatic species. They have also clogged water intake structures, causing billions of dollars in damage to domestic and industrial water supplies.

Humans have deliberately introduced many species with good intentions but disastrous effects. An Asian plant called kudzu, which the U.S. Department of Agriculture once introduced in the southern United States to help control erosion, has taken over large areas of the landscape there **(Figure 43.7)**.

▲ **Figure 43.7 Kudzu, an introduced species, thriving in South Carolina.**

Introduced species are a worldwide problem, contributing to approximately 40% of the extinctions recorded since 1750 and costing billions of dollars each year in damage and control efforts. There are more than 50,000 introduced species in the United States alone.

Overharvesting

The term *overharvesting* refers generally to the harvesting of wild organisms at rates exceeding the ability of their populations to rebound. Species with restricted habitats, such as small islands, are particularly vulnerable to overharvesting. One such species was the great auk, a large, flightless seabird found on islands in the North Atlantic Ocean. By the 1840s, the great auk had been hunted to extinction to satisfy the human demand for its feathers, eggs, and meat.

Also susceptible to overharvesting are large organisms with low reproductive rates, such as elephants, whales, and rhinoceroses. The decline of Earth's largest terrestrial animals, the African elephants, is a classic example of the impact of overhunting. Largely because of the trade in ivory, elephant populations have been declining in most of Africa for the last 50 years. An international ban on the sale of new ivory resulted in increased poaching (illegal hunting), so the ban had little effect in much of central and eastern Africa. Only in South Africa, where once-decimated herds have been well protected for nearly a century, have elephant populations been stable or increasing (see Figure 40.18).

Conservation biologists increasingly use the tools of molecular genetics to track the origins of tissues harvested from endangered species. Researchers at the University of Washington have constructed a DNA reference map for the African elephant using DNA isolated from elephant dung. By comparing this reference map with DNA isolated from samples of ivory harvested either legally or by poachers, they can determine to within a few hundred kilometers where the elephants were killed **(Figure 43.8)**. Such work in Zambia suggested that poaching rates were 30 times higher than previously estimated,

▲ **Figure 43.8 Ecological forensics and elephant poaching.** These severed tusks were part of an illegal shipment of ivory intercepted on its way from Africa to Singapore in 2002. DNA-based evidence showed that the thousands of elephants killed for the tusks came from a relatively narrow east-west band centered in Zambia rather than from across Africa.

leading to improved antipoaching efforts by the Zambian government. Similarly, biologists using phylogenetic analyses of mitochondrial DNA (mtDNA) showed that some whale meat sold in Japanese fish markets came from illegally harvested endangered species (see Figure 20.6).

Many commercially important fish populations, once thought to be inexhaustible, have been decimated by overfishing. Demands for protein-rich food from an increasing human population, coupled with new harvesting technologies, such as long-line fishing and modern trawlers, have reduced these fish populations to levels that cannot sustain further exploitation. Until the past few decades, the North Atlantic bluefin tuna had little commercial value—just a few cents per pound for use in cat food. In the 1980s, however, wholesalers began airfreighting fresh, iced bluefin to Japan for sushi and sashimi. In that market, the fish now brings up to $100 per pound **(Figure 43.9)**. With increased harvesting spurred by such high prices, it took just ten years to reduce the western North Atlantic bluefin population to less than 20% of its 1980 size.

▲ **Figure 43.9 Overharvesting.** North Atlantic bluefin tuna are auctioned in a Japanese fish market.

Global Change

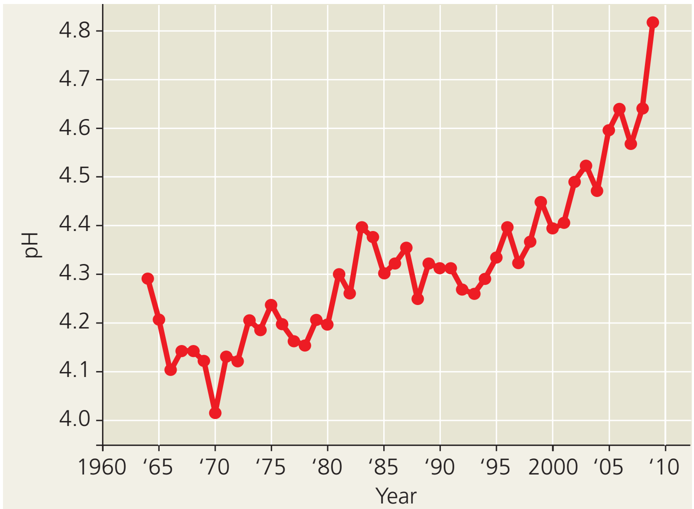
The fourth threat to biodiversity, global change, alters the fabric of Earth's ecosystems at regional to global scales. Global change includes alterations in climate, atmospheric chemistry, and broad ecological systems that reduce the capacity of Earth to sustain life.

One of the first types of global change to cause concern was *acid precipitation*, which is rain, snow, sleet, or fog with a pH less than 5.2. The burning of wood and fossil fuels releases oxides of sulfur and nitrogen that react with water in air, forming sulfuric and nitric acids. The acids eventually fall to Earth's surface, harming some aquatic and terrestrial organisms.

In the 1960s, ecologists determined that lake-dwelling organisms in eastern Canada were dying because of air pollution from factories in the midwestern United States. Newly hatched lake trout, for instance, die when the pH drops below 5.4. Lakes and streams in southern Norway and Sweden were losing fish because of pollution generated in Great Britain and central Europe. By 1980, the pH of precipitation in large areas of North America and Europe averaged 4.0–4.5 and sometimes dropped as low as 3.0. (To review pH, see Concept 2.5.)

Environmental regulations and new technologies have enabled many countries to reduce sulfur dioxide emissions in recent decades. In the United States, sulfur dioxide emissions decreased more than 40% between 1993 and 2009, gradually reducing the acidity of precipitation **(Figure 43.10)**. However, ecologists estimate that it will take decades for aquatic ecosystems to recover. Meanwhile, emissions of nitrogen oxides are increasing in the United States, and emissions of sulfur dioxide and acid precipitation continue to damage forests in Europe.

We will explore the importance of global change for Earth's biodiversity in more detail in Concept 43.4, where we examine such factors as climate change.



▲ **Figure 43.10 Changes in the pH of precipitation at Hubbard Brook, New Hampshire.** Although still acidic, the precipitation in this northeastern U.S. forest has been increasing in pH for more than three decades.

CONCEPT CHECK 43.1

1. Explain why it is too narrow to define the biodiversity crisis as simply a loss of species.
2. Identify the four main threats to biodiversity and explain how each damages diversity.
3. **WHAT IF?** Imagine two populations of a fish species, one in the Mediterranean Sea and one in the Caribbean Sea. Now imagine two scenarios: (1) The populations breed separately, and (2) adults of both populations migrate yearly to the North Atlantic to interbreed. Which scenario would result in a greater loss of genetic diversity if the Mediterranean population were harvested to extinction? Explain your answer.

For suggested answers, see Appendix A.

CONCEPT 43.2

Population conservation focuses on population size, genetic diversity, and critical habitat

Biologists who work on conservation at the population and species levels use two main approaches. One approach focuses on populations that are small and hence often vulnerable. The other emphasizes populations that are declining rapidly, even if they are not yet small.

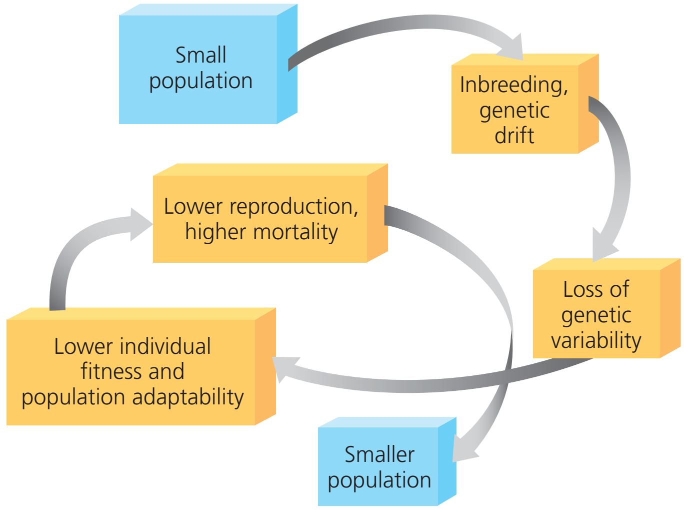
Small-Population Approach

Small populations are particularly vulnerable to overharvesting, habitat loss, and the other threats to biodiversity that you read about in Concept 43.1. After such factors have reduced a population's size, the small size itself can push the population to extinction. Conservation biologists who adopt the small-population approach study the processes that cause extinctions once population sizes have been reduced.

The Extinction Vortex: Evolutionary Implications of Small Population Size

EVOLUTION A small population is vulnerable to inbreeding and genetic drift, which draw the population down an **extinction vortex** toward smaller and smaller population size until no individuals survive **(Figure 43.11)**. A key factor driving the extinction vortex is the loss of the genetic variation that enables evolutionary responses to environmental change, such as the appearance of new strains of pathogens. Both inbreeding and genetic drift can cause a loss of genetic variation (see Chapter 21), and their effects become more harmful as a population shrinks. Inbreeding often reduces fitness because offspring are more likely to be homozygous for harmful recessive traits.

Not all small populations are doomed by low genetic diversity, and low genetic variability does not automatically lead to permanently small populations. For instance, overhunting of northern elephant seals in the 1890s reduced the species to only 20 individuals—clearly a bottleneck with reduced genetic



▲ **Figure 43.11 Processes driving an extinction vortex.**

variation. Since that time, however, the northern elephant seal populations have rebounded to about 150,000 individuals today, though their genetic variation remains relatively low. Thus, low genetic diversity does not always impede population growth.

Case Study: *The Greater Prairie Chicken and the Extinction Vortex*

When Europeans arrived in North America, the greater prairie chicken (*Tympanuchus cupido*) was common from New England to Virginia and across the western prairies of the continent. Land cultivation for agriculture fragmented the populations of this species, and its abundance decreased rapidly (see Chapter 21). Illinois had millions of greater prairie chickens in the 19th century but fewer than 50 by 1993. Researchers found that the decline in the Illinois population was associated with a decrease in fertility. As a test of the extinction vortex hypothesis, scientists increased the genetic variation of the Illinois population by importing 271 birds from larger populations elsewhere **(Figure 43.12)**. The Illinois population rebounded, confirming that it had been on its way to extinction until rescued by the transfusion of genetic variation.

Minimum Viable Population Size

How small does a population have to be before it starts down an extinction vortex? The answer depends on the type of organism and other factors. Large predators that feed high on the food chain usually require extensive individual ranges, resulting in low population densities. Therefore, not all rare species concern conservation biologists. All populations, however, require some minimum size to remain viable.

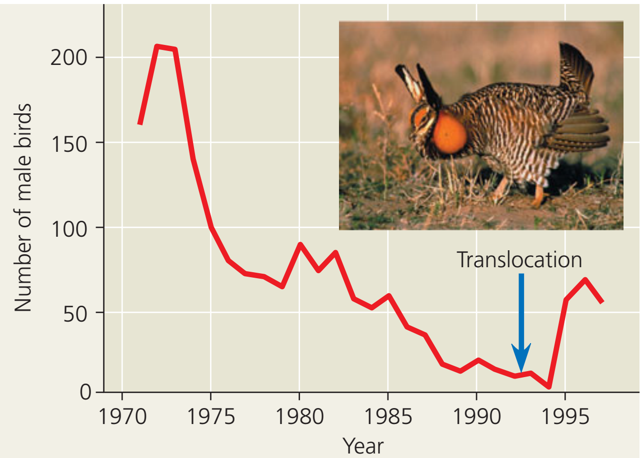
The minimal population size at which a species is able to sustain its numbers is known as the **minimum viable population (MVP)**. MVP is usually estimated for a given species using computer models that integrate many factors. The calculation may include, for instance, an estimate of how many individuals in a small population are likely to be killed by a natural

▼ Figure 43.12 Inquiry

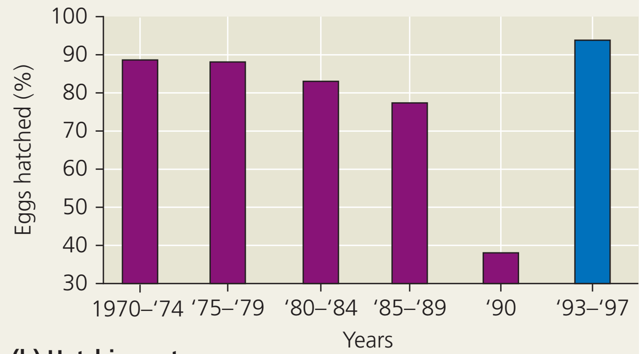
What caused the drastic decline of the Illinois greater prairie chicken population?

Experiment Researchers had observed that the population collapse of the greater prairie chicken was mirrored in a reduction in fertility, as measured by the hatching rate of eggs. Comparison of DNA samples from the Jasper County, Illinois, population with DNA from feathers in museum specimens showed that genetic variation had declined in the study population (see Figure 21.11). In 1992, Ronald Westemeier, Jeffrey Brawn, and colleagues began translocating prairie chickens from Minnesota, Kansas, and Nebraska in an attempt to increase genetic variation.

Results After translocation (blue arrow), the viability of eggs rapidly increased, and the population rebounded.



(a) Population dynamics



(b) Hatching rate

Conclusion Reduced genetic variation had started the Jasper County population of prairie chickens down the extinction vortex.

Source R. L. Westemeier et al., Tracking the long-term decline and recovery of an isolated population, *Science* 282:1695–1698 (1998).

Inquiry in Action Read and analyze the original paper in *Inquiry in Action: Interpreting Scientific Papers*.

WHAT IF? Given the success of using transplanted birds as a tool for increasing the percentage of hatched eggs in Illinois, why wouldn't you transplant additional birds immediately to Illinois?

catastrophe such as a storm. Once in the extinction vortex, two or three consecutive years of bad weather could finish off a population that is already below its MVP.

Effective Population Size

Genetic variation is the key issue in the small-population approach. The *total* size of a population may be misleading because only certain members of the population breed successfully and pass their alleles on to offspring. Therefore, a meaningful estimate of MVP requires the researcher to determine the **effective population size**, which is based on the breeding potential of the population.

The following formula incorporates the sex ratio of breeding individuals into the estimate of effective population size, abbreviated N_e:

$$N_e = \frac{4N_fN_m}{N_f + N_m}$$

where N_f and N_m are, respectively, the number of females and the number of males that successfully breed. If we apply this formula to an idealized population whose total size is 1,000 individuals, N_e will also be 1,000 if every individual breeds and the sex ratio is 500 females to 500 males. In this case, $N_e = (4 \times 500 \times 500)/(500 + 500) = 1{,}000$. Any deviation from these conditions (not all individuals breed or there is not a 1:1 sex ratio) reduces N_e. For instance, if the total population size is 1,000 but only 400 females and 400 males breed, then $N_e = (4 \times 400 \times 400)/(400 + 400) = 800$, or 80% of the total population. Numerous life history traits can influence N_e, and alternative formulas for estimating N_e take into account factors such as family size, age at maturation, genetic relatedness among population members, the effects of gene flow between geographically separated populations, and population fluctuations.

In actual study populations, N_e is always some fraction of the total population. Thus, simply determining the total number of individuals in a small population does not provide a good measure of whether the population is large enough to avoid extinction. Whenever possible, conservation programs attempt to sustain total population sizes that include at least the minimum viable number of *reproductively active* individuals. The conservation goal of sustaining effective population size (N_e) above MVP stems from the concern that populations retain enough genetic diversity to adapt as their environment changes.

Case Study: *Analysis of Grizzly Bear Populations*

One of the first population viability analyses was conducted in 1978 by Mark Shaffer, of Duke University, as part of a long-term study of grizzly bears in Yellowstone National Park and its surrounding areas **(Figure 43.13)**. A threatened species in the United States, the grizzly bear (*Ursus arctos horribilis*) is currently found in only 4 of the 48 contiguous states. Its populations in those states have been drastically reduced and fragmented. In 1800, an estimated 100,000 grizzlies ranged over about 500 million ha of habitat, while today only about 1,000 individuals in six relatively isolated populations range over less than 5 million ha.

▲ **Figure 43.13 Long-term monitoring of a grizzly bear population.** The ecologist is fitting this tranquilized bear with a radio collar so that the bear's movements can be compared with those of other grizzlies in the Yellowstone National Park population.

Shaffer attempted to determine viable sizes for the Yellowstone grizzly population. Using life history data obtained for individual Yellowstone bears over a 12-year period, he simulated the effects of environmental factors on survival and reproduction. His models predicted that, given a suitable habitat, a Yellowstone grizzly bear population of 70–90 individuals would have about a 95% chance of surviving for 100 years. A slightly larger population of only 100 bears would have a 95% chance of surviving for twice as long, about 200 years.

How does the actual size of the Yellowstone grizzly population compare with Shaffer's predicted MVP? A current estimate puts the total grizzly bear population in the greater Yellowstone ecosystem at about 500 individuals. The relationship of this estimate to the effective population size, N_e, depends on several factors. Usually, only a few dominant males breed, and it may be difficult for them to locate females, since individuals inhabit such large areas. Moreover, females may reproduce only when there is abundant food. As a result, N_e is only about 25% of the total population size, or about 125 bears.

Because small populations tend to lose genetic variation over time, researchers have analyzed proteins, mtDNA, and short tandem repeats (see Chapter 18) to assess genetic variability in the Yellowstone grizzly bear population. All results to date indicate that the Yellowstone population has less genetic variability than other grizzly bear populations in North America.

How might conservation biologists increase the effective size and genetic variation of the Yellowstone grizzly bear population? Migration between isolated populations of grizzlies could increase both effective and total population sizes. Computer models predict that introducing only two unrelated bears each decade into a population of 100 individuals would reduce the loss of genetic variation by about half. For the grizzly bear, and probably for many other species with small populations, finding ways to promote dispersal among populations may be one of the most urgent conservation needs.

This case study and that of the greater prairie chicken bridge small-population models and practical applications in conservation. Next, we look at an alternative approach to understanding the biology of extinction.

Declining-Population Approach

The declining-population approach focuses on threatened and endangered populations that show a downward trend, even if the population is far above its minimum viable population. The distinction between a declining population, which may not be small, and a small population, which may not be declining, is less important than the different priorities of the two approaches. The small-population approach emphasizes smallness itself as an ultimate cause of a population's extinction, especially through the loss of genetic diversity. In contrast, the declining-population approach emphasizes the environmental factors that caused a population decline in the first place. If, for instance, an area is deforested, then species that depend on trees will decline in abundance and become locally extinct, whether or not they retain genetic variation. The following case study is one example of how the declining-population approach has been applied to the conservation of an endangered species.

Case Study: *Decline of the Red-Cockaded Woodpecker*

The red-cockaded woodpecker (*Picoides borealis*) is found only in the southeastern United States. It requires mature pine forests, preferably ones dominated by the longleaf pine, for its habitat. Most woodpeckers nest in dead trees, but the red-cockaded woodpecker drills its nest holes in mature, living pine trees. It also drills small holes around the entrance to its nest cavity, which causes resin from the tree to ooze down the trunk. The resin seems to repel predators, such as corn snakes, that eat bird eggs and nestlings.

Another critical habitat factor for the red-cockaded woodpecker is that the undergrowth of plants around the pine trunks must be low **(Figure 43.14a)**. Breeding birds tend to abandon nests when vegetation among the pines is thick and higher than about 4.5 m **(Figure 43.14b)**. Apparently, the birds need a clear flight path between their home trees and the neighboring feeding grounds. Periodic fires have historically swept through longleaf pine forests, keeping the undergrowth low.

One factor leading to the woodpecker's decline has been the destruction or fragmentation of suitable habitats by logging and agriculture. By recognizing key habitat factors, protecting some longleaf pine forests, and using controlled fires to reduce forest undergrowth, conservation managers have helped restore habitat that can support viable populations.

Sometimes conservation managers also help species colonize restored habitats. Because red-cockaded woodpeckers take months to excavate nesting cavities, researchers performed an experiment to see whether providing cavities for the birds would make them more likely to use a site. The

(a) Forests that can sustain red-cockaded woodpeckers have low undergrowth.

(b) Forests that cannot sustain red-cockaded woodpeckers have high, dense undergrowth that interferes with the woodpeckers' access to feeding grounds.

▲ **Figure 43.14 A habitat requirement of the red-cockaded woodpecker.**

? *How is habitat disturbance necessary for the long-term survival of the woodpecker?*

researchers constructed cavities in pine trees at 20 restored sites and compared nesting rates there with rates in sites without constructed cavities. The results were dramatic. Cavities in 18 of the 20 sites with constructed cavities were colonized by red-cockaded woodpeckers, and new breeding groups formed only in those sites. Based on this experiment, conservationists initiated a habitat maintenance program that included controlled burning and excavation of new nesting cavities, enabling this endangered species to begin to recover.

Weighing Conflicting Demands

Determining population numbers and habitat needs is only part of a strategy to save species. Scientists also need to weigh a species' needs against other conflicting demands. Conservation biology often highlights the relationship between science, technology, and society. For example, an ongoing, sometimes bitter debate in the western United States pits habitat preservation for wolf, grizzly bear, and bull trout populations against job opportunities in the grazing and resource extraction industries. Programs that restocked wolves in Yellowstone National Park remain controversial for people concerned about human safety and for many ranchers concerned with potential loss of livestock outside the park.

Large, high-profile vertebrates are not always the focal point in such conflicts, but habitat use is almost always the issue. Should work proceed on a new highway bridge if it destroys the only remaining habitat of a species of freshwater mussel? If you owned a coffee plantation growing varieties that thrive in bright sunlight, would you be willing to change to shade-tolerant varieties that produce less coffee per hectare but can grow beneath trees that support large numbers of songbirds?

Another important consideration is the ecological role of a species. Because we cannot save every endangered species, we must determine which species are most important for conserving biodiversity as a whole. Identifying keystone species and finding ways to sustain their populations can be central to maintaining communities and ecosystems. In most situations, we must look beyond a species and consider the whole community and ecosystem as an important unit of biodiversity.

CONCEPT CHECK 43.2

1. How does the reduced genetic diversity of small populations make them more vulnerable to extinction?
2. If there was a total of 50 individuals in the two Illinois populations of greater prairie chickens in 1993, what was the effective population size if 15 females and 5 males bred?
3. **WHAT IF?** In 2011, at least ten grizzly bears in the greater Yellowstone ecosystem were killed through contact with people. Three things caused many of these deaths: collisions with automobiles, hunters (of other animals) shooting when charged by a female grizzly bear with cubs nearby, and conservation managers killing bears that attacked livestock repeatedly. If you were a conservation manager, what steps might you take to minimize such encounters in Yellowstone?

For suggested answers, see Appendix A.

CONCEPT **43.3**

Landscape and regional conservation help sustain biodiversity

Although conservation efforts historically focused on saving individual species, efforts today often seek to sustain the biodiversity of entire communities, ecosystems, and landscapes. Such a broad view requires applying not just the principles of community, ecosystem, and landscape ecology but aspects of human population dynamics and economics as well. The goals of landscape ecology (see Chapter 40) include projecting future patterns of landscape use and making biodiversity conservation part of land-use planning.

Landscape Structure and Biodiversity

The biodiversity of a given landscape is in large part a function of the structure of the landscape. Understanding landscape structure is critically important in conservation because many species use more than one kind of ecosystem, and many live on the borders between ecosystems.

Fragmentation and Edges

The boundaries, or *edges*, between ecosystems—such as between a lake and the surrounding forest or between cropland and suburban housing tracts—are defining features of landscapes **(Figure 43.15)**. An edge has its own set of physical conditions, which differ from those on either side of it. The soil surface of an edge between a forest patch and a burned area receives more sunlight and is usually hotter and drier than the forest interior, but it is cooler and wetter than the soil surface in the burned area.

Some organisms thrive in edge communities because they gain resources from both adjacent areas. The ruffed grouse (*Bonasa umbellus*) is a bird that needs forest habitat for nesting, winter food, and shelter, but it also needs forest openings with dense shrubs and herbs for summer food.

Ecosystems in which edges arise from human alterations often have reduced biodiversity and a preponderance of edge-adapted species. For example, white-tailed deer thrive in edge habitats, where they can browse on woody shrubs; deer populations often expand when forests are logged and more edges are generated. The brown-headed cowbird (*Molothrus ater*) is an edge-adapted species that lays its eggs in the nests of other birds, often migratory songbirds. Cowbirds need forests, where they can parasitize the nests of other birds, and open fields, where they forage on seeds and insects. Consequently, their populations are growing where forests are being cut and fragmented, creating more edge habitat and open land. Increasing cowbird parasitism and habitat loss are correlated with declining populations of several of the cowbird's host species.

The influence of fragmentation on the structure of communities has been explored since 1979 in the long-term Biological Dynamics of Forest Fragments Project. Located in the heart of the Amazon River basin, the study area consists of isolated fragments of tropical rain forest separated from surrounding continuous forest by distances of 80–1,000 m **(Figure 43.16)**. Numerous researchers working on this project have clearly documented the effects of this fragmentation on organisms ranging from bryophytes to beetles to birds. They have consistently found that species adapted to forest interiors show the greatest declines when patches are the smallest, suggesting that landscapes dominated by small fragments will support fewer species.

Corridors That Connect Habitat Fragments

In fragmented habitats, the presence of a **movement corridor**, a narrow strip or series of small clumps of habitat connecting otherwise isolated patches, can be extremely important for conserving biodiversity. Riparian habitats often serve as corridors, and in some nations, government policy prohibits altering these habitats. In areas of heavy human use, artificial corridors are sometimes constructed. Bridges or tunnels, for instance, can reduce the number of animals killed trying to cross highways **(Figure 43.17)**.

Movement corridors can also promote dispersal and reduce inbreeding in declining populations. Corridors have been

▲ **Figure 43.15 Edges between ecosystems.** Grasslands give way to forest ecosystems in Yellowstone National Park.

▲ **Figure 43.16 Amazon rain forest fragments created as part of the Biological Dynamics of Forest Fragments Project.**

▲ **Figure 43.17 An artificial corridor.** This bridge in Banff National Park, Canada, helps animals cross a human-created barrier.

shown to increase the exchange of individuals among populations of many organisms, including butterflies, voles, and aquatic plants. Corridors are especially important to species that migrate between different habitats seasonally. However, a corridor can also be harmful—for example, by allowing the spread of disease. In a 2003 study, a scientist at the University of Zaragoza, Spain, showed that habitat corridors facilitate the movement of disease-carrying ticks among forest patches in northern Spain. All the effects of corridors are not yet understood, and their impact is an area of active research in conservation biology.

Establishing Protected Areas

Conservation biologists are applying their understanding of landscape dynamics in establishing protected areas to slow biodiversity loss. Currently, governments have set aside about 7% of the world's land in various forms of reserves. Choosing where to place nature reserves and how to design them poses many challenges. Should the reserve be managed to minimize the risks of fire and predation to a threatened species? Or should the reserve be left as natural as possible, with such processes as fires ignited by lightning allowed to play out on their own? This is just one of the debates that arise among people who share an interest in the health of national parks and other protected areas.

Preserving Biodiversity Hot Spots

In deciding which areas are of highest conservation priority, biologists often focus on hot spots of biodiversity. A **biodiversity hot spot** is a relatively small area with numerous endemic species (species found nowhere else in the world) and a large number of endangered and threatened species **(Figure 43.18)**. Nearly 30% of all bird species can be found in hot spots that make up only about 2% of Earth's land area. Together, the "hottest" of the terrestrial biodiversity hot spots total less than 1.5% of Earth's land but are home to more than a third of all species of plants, amphibians, reptiles (including birds), and mammals. Aquatic ecosystems also have hot spots, such as coral reefs and certain river systems.

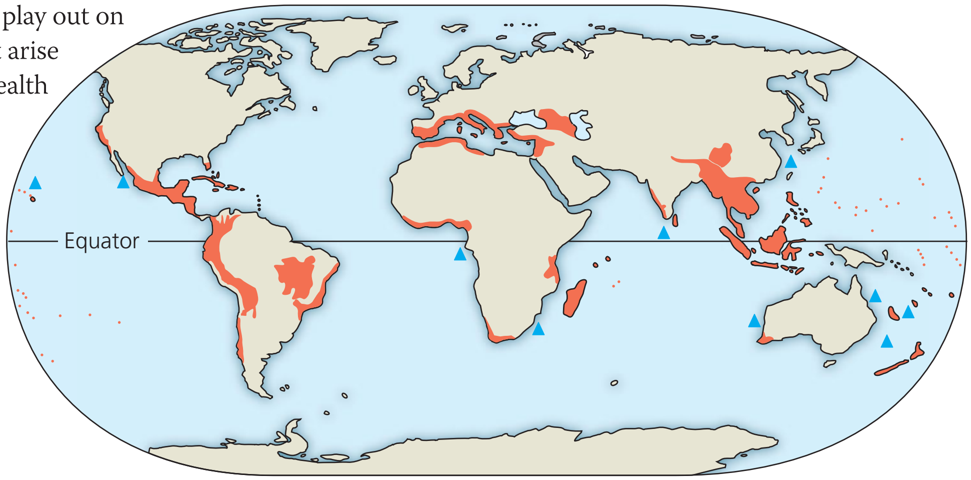
Biodiversity hot spots are good choices for nature reserves, but identifying them is not always simple. One problem is that a hot spot for one taxonomic group, such as butterflies, may not be a hot spot for some other taxonomic group, such as birds. Designating an area as a biodiversity hot spot is often biased toward saving vertebrates and plants, with less attention paid to invertebrates and microorganisms. Some biologists are also concerned that the hot-spot strategy places too much emphasis on such a small fraction of Earth's surface.

Global change makes the task of preserving hot spots even more challenging because the conditions that favor a particular community may not be found in the same location in the future. The biodiversity hot spot in the southwest corner of Australia (see Figure 43.18) holds thousands of species of endemic plants and numerous endemic vertebrates. Researchers recently concluded that between 5% and 25% of the plant species they examined may become extinct by 2080 because the plants will be unable to tolerate the increased dryness predicted for this region.

Philosophy of Nature Reserves

Nature reserves are biodiversity islands in a sea of habitat degraded by human activity. Protected "islands" are not isolated from their surroundings, however, and the nonequilibrium model (see Chapter 41) applies to nature reserves as well as to the larger landscapes around them.

An earlier policy—that protected areas should be set aside to remain unchanged forever—was based on the concept that ecosystems are balanced, self-regulating units. However, disturbance is common in all ecosystems (see Chapter 41), and management policies that ignore natural disturbances or attempt to prevent them have generally failed. For instance, setting aside an area of a fire-dependent community, such as a



▲ **Figure 43.18 Earth's terrestrial (■) and marine (▲) biodiversity hot spots.**

portion of a tallgrass prairie, chaparral, or dry pine forest, with the intention of saving it is unrealistic if periodic burning is excluded. Without the dominant disturbance, the fire-adapted species are usually outcompeted and biodiversity is reduced.

An important conservation question is whether to create numerous small reserves or fewer large reserves. Small, unconnected reserves may slow the spread of disease between populations. One argument for large reserves is that large, far-ranging animals with low-density populations, such as the grizzly bear, require extensive habitats. Large reserves also have proportionately smaller perimeters than small reserves and are therefore less affected by edges.

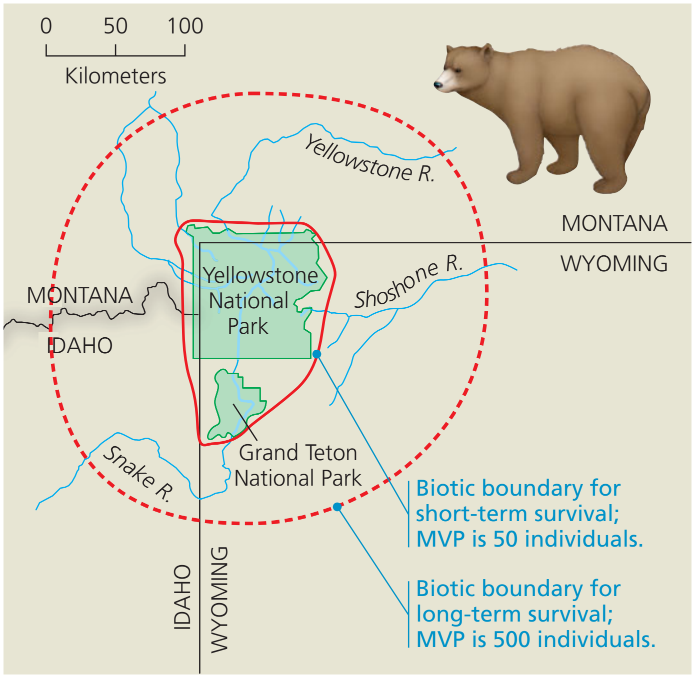
As conservation biologists have learned more about the requirements for achieving minimum viable populations for endangered species, they have realized that most national parks and other reserves are far too small. The area needed for the long-term survival of the Yellowstone grizzly bear population, for instance, is more than ten times the combined area of Yellowstone and Grand Teton National Parks **(Figure 43.19)**. Areas of private and public land surrounding reserves will likely have to contribute to biodiversity conservation.

Zoned Reserves

Several nations have adopted a zoned reserve approach to landscape management. A **zoned reserve** is an extensive region that includes relatively undisturbed areas surrounded by areas that have been changed by human activity and are used for economic gain. The key challenge of the zoned reserve approach is to develop a social and economic climate in the surrounding lands that is compatible with the long-term viability of the protected core. These surrounding areas continue to support human activities, but regulations prevent the types of extensive alterations likely to harm the protected area. As a result, the surrounding habitats serve as buffer zones against further intrusion into the undisturbed area.

The small Central American nation of Costa Rica has become a world leader in establishing zoned reserves **(Figure 43.20)**. An agreement initiated in 1987 reduced Costa Rica's international debt in return for land preservation there. The agreement resulted in eight zoned reserves, called "conservation areas," that contain designated national park land. Costa Rica is making progress toward managing its zoned reserves, and the buffer zones provide a steady, lasting supply of forest products, water, and hydroelectric power while also supporting sustainable agriculture and tourism, both of which employ local people.

Although marine ecosystems have also been heavily affected by human exploitation, reserves in the ocean are far less common than reserves on land. Many fish populations around the world have collapsed as increasingly sophisticated equipment puts nearly all potential fishing grounds within human reach. In response, scientists at the University of York, England, have proposed establishing marine reserves around the world that would be off limits to fishing. They present strong evidence that a patchwork of marine reserves can serve as a means of both increasing fish populations within the reserves and improving fishing success in nearby areas. Their proposed system is a modern application of a centuries-old practice in the Fiji Islands in which some areas have historically remained closed to fishing—a traditional example of the zoned reserve concept.



▲ **Figure 43.19 Biotic boundaries for grizzly bears in Yellowstone and Grand Teton National Parks.** The biotic boundaries (solid and dashed red lines) surround the areas needed to support minimum viable populations of 50 and 500 bears. Even the smaller of these areas is larger than the two parks.

▲ **Figure 43.20 Zoned reserves in Costa Rica.** Boundaries of the zoned reserves are indicated by black outlines.

▲ **Figure 43.21 A diver measuring coral in the Florida Keys National Marine Sanctuary.**

The United States adopted such a system in creating a set of 13 national marine sanctuaries, including the Florida Keys National Marine Sanctuary, which was established in 1990 **(Figure 43.21)**. Populations of marine organisms, including fishes and lobsters, recovered quickly after harvests were banned in the 9,500-km^2 reserve. Larger and more abundant fish now produce larvae that help repopulate reefs and improve fishing outside the sanctuary. The increased marine life within the sanctuary also makes it a favorite for recreational divers, increasing the economic value of this zoned reserve.

CONCEPT CHECK 43.3

1. What is a biodiversity hot spot?
2. How do zoned reserves provide economic incentives for long-term conservation of protected areas?
3. **WHAT IF?** Suppose a developer proposes to clear-cut a forest that serves as a corridor between two parks. To compensate, the developer also proposes to add the same area of forest to one of the parks. As a professional ecologist, how might you argue for retaining the corridor?

For suggested answers, see Appendix A.

CONCEPT 43.4

Earth is changing rapidly as a result of human actions

As we've discussed, landscape and regional conservation help protect habitats and preserve species. However, environmental changes that result from human activities are creating new challenges. As a consequence of human-caused climate change, for example, the place where a vulnerable species is found today may not be the same as the one needed for preservation in the future. What would happen if *many* habitats on Earth changed so quickly that the locations of preserves today were unsuitable for their species in 10, 50, or 100 years? Such a scenario is increasingly likely.

The rest of this section describes three types of environmental change that threaten biodiversity: nutrient enrichment, toxin accumulation, and climate change. The impacts of these and other changes are evident not just in human-dominated ecosystems, such as cities and farms, but also in the most remote ecosystems on Earth.

Nutrient Enrichment

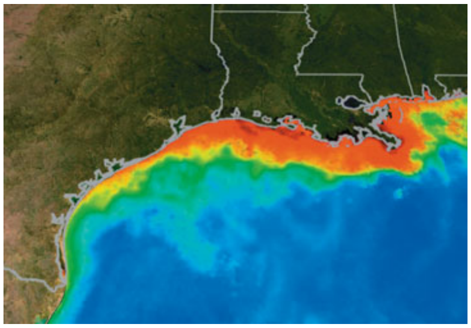
Human activity often removes nutrients from one part of the biosphere and adds them to another. Someone eating strawberries in Washington, DC, consumes nutrients that only days before were in the soil in California; a short time later, some of these nutrients will be in the Potomac River, having passed through the person's digestive system and a local sewage treatment facility.

Farming is an example of how human activities are altering the environment through the enrichment of nutrients. After vegetation is cleared from an area, the existing reserve of nutrients in the soil is sufficient to grow crops for only a brief period because a substantial fraction of these nutrients is exported from the area in crop biomass. For this reason, farmers typically add fertilizers to increase crop yields.

Nitrogen is the main nutrient element lost through agriculture (see Figure 42.13). Plowing mixes the soil and speeds up decomposition of organic matter, releasing nitrogen that is then removed when crops are harvested. Applied fertilizers make up for the loss of usable nitrogen from agricultural ecosystems. However, without plants to take up nitrates from the soil, the nitrates are likely to be leached from the ecosystem (see Figure 42.14). Recent studies indicate that human activities have more than doubled Earth's supply of fixed nitrogen available to primary producers.

A problem arises when the nutrient level in an ecosystem exceeds the **critical load**, the amount of added nutrient, usually nitrogen or phosphorus, that can be absorbed by plants without damaging ecosystem integrity. For example, nitrogenous minerals in the soil that exceed the critical load eventually leach into groundwater or run off into freshwater and marine ecosystems, sometimes contaminating water supplies and killing fish. Nitrate concentrations in groundwater are increasing in most agricultural regions, sometimes reaching levels that are unsafe for drinking.

Many rivers contaminated with nitrates and ammonium from agricultural runoff and sewage drain into the Atlantic Ocean, with the highest inputs coming from northern Europe and the central United States. The Mississippi River carries nitrogen pollution to the Gulf of Mexico, fueling a phytoplankton bloom each summer. When the phytoplankton die, their decomposition by oxygen-using organisms creates an extensive "dead zone" of low oxygen concentrations along the Gulf coast



▲ **Figure 43.22 A phytoplankton bloom arising from nitrogen pollution in the Mississippi basin that leads to a dead zone.** In this satellite image from 2004, red and orange represent high concentrations of phytoplankton in the Gulf of Mexico.

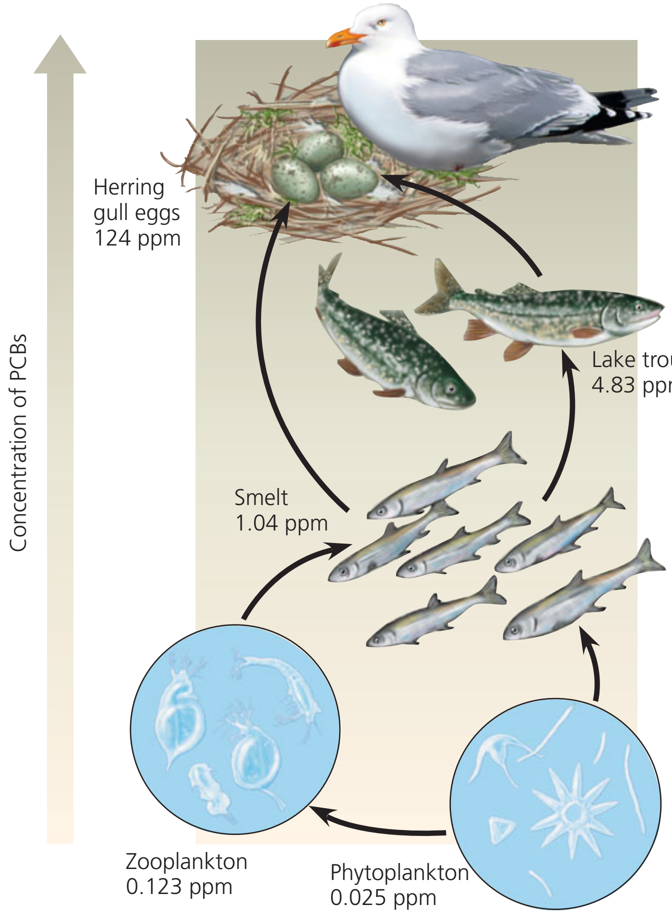
(Figure 43.22). Fish and other marine animals disappear from some of the most economically important waters in the United States. To reduce the size of the dead zone, farmers have begun using fertilizers more efficiently, and managers are restoring wetlands in the Mississippi watershed, two changes stimulated by the results of ecosystem experiments.

Nutrient runoff can also lead to the eutrophication of lakes (see Concept 42.2). The bloom and subsequent die-off of algae and cyanobacteria and the ensuing depletion of oxygen are similar to what occurs in a marine dead zone. Such conditions threaten the survival of organisms. For example, eutrophication of Lake Erie coupled with overfishing wiped out commercially important fishes such as blue pike, whitefish, and lake trout by the 1960s. Since then, tighter regulations on the dumping of sewage and other wastes into the lake have enabled some fish populations to rebound, but many native species of fish and invertebrates have not recovered.

Toxins in the Environment

Human activities release an immense variety of toxic chemicals, including thousands of synthetic compounds previously unknown in nature, with little regard for the ecological consequences. Organisms acquire toxic substances from the environment along with nutrients and water. Some of the poisons are metabolized or excreted, but others accumulate in specific tissues, often fat. One of the reasons accumulated toxins are particularly harmful is that they become more concentrated in successive trophic levels of a food web. This phenomenon, called **biological magnification**, occurs because the biomass at any given trophic level is produced from a much larger biomass ingested from the level below (see Concept 42.3). Thus, top-level carnivores tend to be most severely affected by toxic compounds in the environment.

One class of industrially synthesized compounds that have demonstrated biological magnification are the chlorinated hydrocarbons, which include the industrial chemicals called PCBs (polychlorinated biphenyls) and many pesticides, such as DDT. Current research implicates many of these compounds in endocrine system disruption in a large number of animal



▲ **Figure 43.23 Biological magnification of PCBs in a Great Lakes food web.**

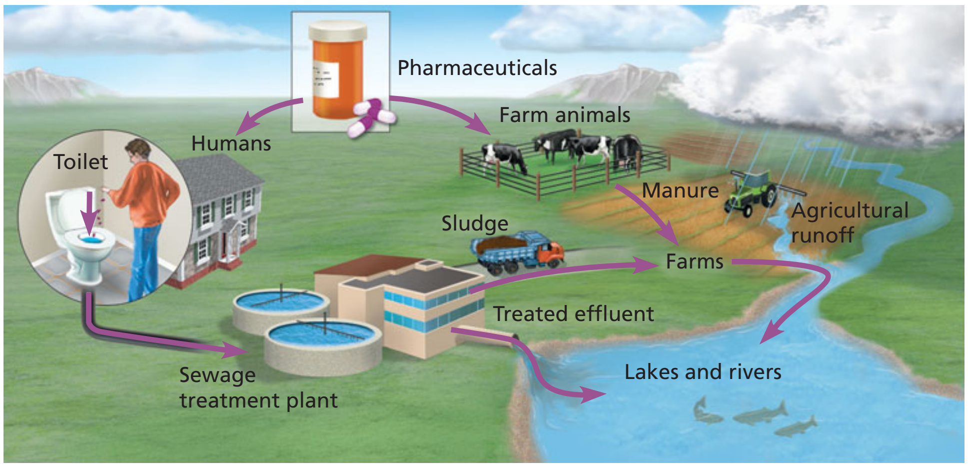
species, including humans. Biological magnification of PCBs has been found in the food web of the Great Lakes, where the concentration of PCBs in herring gull eggs, at the top of the food web, is nearly 5,000 times that in phytoplankton, at the base of the food web **(Figure 43.23)**.

An infamous case of biological magnification that harmed top-level carnivores involved DDT, a chemical used to control insects such as mosquitoes and agricultural pests. In the decade after World War II, the use of DDT grew rapidly; its ecological consequences were not yet fully understood. By the 1950s, scientists were learning that DDT persists in the environment and is transported by water to areas far from where it is applied. One of the first signs that DDT was a serious environmental problem was a decline in the populations of pelicans, ospreys, and eagles, birds that feed at the top of food webs. The accumulation of DDT (and DDE, a product of its breakdown) in the tissues of these birds interfered with the deposition of calcium in their eggshells. When the birds tried to incubate their eggs, the weight of the parents broke the shells of affected eggs, resulting in catastrophic declines in the birds' reproduction rates. Rachel Carson's book *Silent Spring* helped bring the problem to public attention in the 1960s **(Figure 43.24)**, and DDT was banned in the United States in 1971. A dramatic recovery in populations of the affected bird species followed.

▶ Figure 43.24 Rachel Carson. Through her writing and her testimony before the U.S. Congress, biologist and author Rachel Carson helped promote a new environmental ethic. Her efforts led to a ban on DDT use in the United States and stronger controls on the use of other chemicals.

In countries throughout much of the tropics, DDT is still used to control the mosquitoes that spread malaria and other diseases. Societies there face a trade-off between saving human lives and protecting other species. The best approach seems to be to apply DDT sparingly and to couple its use with mosquito netting and other low-technology solutions. The complicated history of DDT illustrates the importance of understanding the ecological connections between diseases and communities (see Concept 41.5).

Pharmaceuticals make up another group of toxins in the environment, one that is a growing concern among ecologists. The use of over-the-counter and prescription drugs has risen in recent years, particularly in industrialized nations. People who consume such products excrete residual chemicals in their waste and may also dispose of unused drugs improperly, such as in their toilets or sinks. Drugs that are not broken down in sewage treatment plants may then enter rivers and lakes with the material discharged from these plants. Growth-promoting drugs given to farm animals can also enter rivers and lakes with agricultural runoff. As a consequence, many pharmaceuticals are spreading in low concentrations across the world's freshwater ecosystems **(Figure 43.25)**.



▲ Figure 43.25 Sources and movements of pharmaceuticals in the environment.

Among the pharmaceuticals that ecologists are studying are the sex steroids, including forms of estrogen used for birth control. Some fish species are so sensitive to certain estrogens that concentrations of a few parts per trillion in their water can alter sexual differentiation and shift the female-to-male sex ratio toward females. Researchers in Ontario, Canada, conducted a seven-year experiment in which they applied the synthetic estrogen used in contraceptives to a lake in very low concentrations (5–6 ng/L). They found that chronic exposure of the fathead minnow (*Pimephales promelas*) to the estrogen led to feminization of males and a near extinction of the species from the lake.

Many toxins cannot be degraded by microorganisms and persist in the environment for years or even decades. In other cases, chemicals released into the environment may be relatively harmless but are converted to more toxic products by reaction with other substances, by exposure to light, or by the metabolism of microorganisms. Mercury, a by-product of plastic production and coal-fired power generation, has been routinely expelled into rivers and the sea in an insoluble form. Bacteria in the bottom mud convert the waste to methylmercury (CH_3Hg^+), an extremely toxic water-soluble compound that accumulates in the tissues of organisms, including humans who consume fish from the contaminated waters.

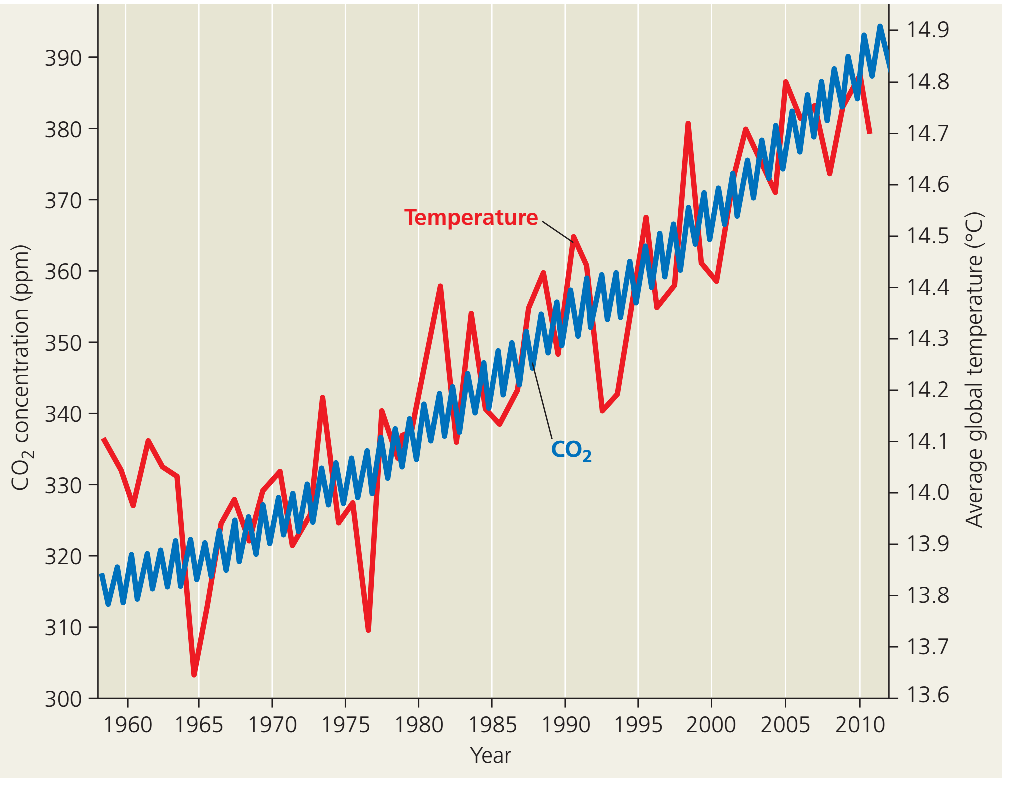
Greenhouse Gases and Climate Change

Human activities release a variety of gaseous waste products. People once thought that the vast atmosphere could absorb these materials indefinitely, but we now know that such additions can cause fundamental changes to the atmosphere and to its interactions with the rest of the biosphere. In this section, we'll examine how increasing concentrations of carbon dioxide and other greenhouse gases may affect species and ecosystems.

Since the Industrial Revolution, the concentration of CO_2 in the atmosphere has been increasing as a result of the burning of fossil fuels and deforestation. Scientists estimate that the average CO_2 concentration in the atmosphere before 1850 was about 274 ppm. In 1958, a monitoring station began taking very accurate measurements on Hawaii's Mauna Loa peak, a location far from cities and high enough for the atmosphere to be well mixed. At that time, the CO_2 concentration was 316 ppm **(Figure 43.26)**. Today, it exceeds 390 ppm, an increase of more than 40% since the mid-19th century. In the **Scientific Skills Exercise**, you can graph and interpret changes in CO_2 concentration that occur during the course of a year and over longer periods.

The marked increase in the concentration of atmospheric CO_2 over the last 150 years concerns scientists because

▶ **Figure 43.26 Increase in atmospheric carbon dioxide concentration at Mauna Loa, Hawaii, and average global temperatures.** Aside from normal seasonal fluctuations, the CO_2 concentration (blue curve) has increased steadily from 1958 to 2011. Though average global temperatures (red curve) fluctuated a great deal over the same period, there is a clear warming trend.



Scientific Skills Exercise

Graphing Cyclic Data

How Does the Atmospheric CO_2 Concentration Change During a Year and from Decade to Decade? The blue curve in Figure 43.26 shows how the concentration of CO_2 in Earth's atmosphere has changed over a span of more than 50 years. For each year in that span, two data points are plotted, one in May and one in November. A more detailed picture of the change in CO_2 concentration can be obtained by looking at measurements made at more frequent intervals. In this exercise, you'll graph monthly CO_2 concentrations for three years over three decades.

Data from the Study The data in the table below are average CO_2 concentrations (in parts per million) at the Mauna Loa monitoring station for each month in 1990, 2000, and 2010.

Month	1990	2000	2010
January	353.79	369.25	388.45
February	354.88	369.50	389.82
March	355.65	370.56	391.08
April	356.27	371.82	392.46
May	359.29	371.51	392.95
June	356.32	371.71	392.06
July	354.88	369.85	390.13
August	352.89	368.20	388.15
September	351.28	366.91	386.80
October	351.59	366.91	387.18
November	353.05	366.99	388.59
December	354.27	369.67	389.68

Interpret the Data

1. Plot the data for all three years on one graph. Select a type of graph that is appropriate for these data, and choose a vertical-axis scale that allows you to clearly see the patterns of CO_2 concentration changes, both during each year and from decade to decade. (For additional information about graphs, see the Scientific Skills Review in Appendix F and in the Study Area in MasteringBiology.)
2. Within each year, what is the pattern of change in CO_2 concentration? Why does this pattern occur?
3. The measurements taken at Mauna Loa represent average atmospheric CO_2 concentrations for the Northern Hemisphere. Suppose you could measure CO_2 concentrations under similar conditions in the Southern Hemisphere. What pattern would you expect to see in those measurements over the course of a year? Explain.
4. In addition to the changes within each year, what changes in CO_2 concentration occurred between 1990 and 2010? Calculate the average CO_2 concentration for the 12 months of each year. By what percentage did this average change from 1990 to 2000 and from 1990 to 2010?

Data from National Oceanic & Atmospheric Administration, Earth System Research Laboratory, Global Monitoring Division

MB A version of this Scientific Skills Exercise can be assigned in MasteringBiology.

of its link to increased global temperature. Much of the solar radiation that strikes the planet is reflected back into space. Although CO_2, methane, water vapor, and other gases in the atmosphere are transparent to visible light, they intercept and absorb much of the infrared radiation Earth emits, re-reflecting some of it back toward Earth. This process retains some of the solar heat. If it were not for this **greenhouse effect**, the average air temperature at Earth's surface would be a frigid −18°C (−0.4°F), and most life as we know it could not exist.

For more than a century, scientists have studied how greenhouse gases warm Earth and how fossil fuel burning could contribute to the warming. Most scientists are convinced that such warming is already occurring and will increase rapidly this century (see Figure 43.26). Global models predict that by the end of the 21st century, the atmospheric CO_2 concentration will have more than doubled, increasing average global temperature by about 3°C (5°F).

Supporting these models is a correlation between CO_2 levels and temperatures in prehistoric times. One way climatologists estimate past CO_2 concentrations is to measure CO_2 levels in bubbles trapped in glacial ice, some of which are 700,000 years old. Prehistoric temperatures are inferred by several methods, including analysis of past vegetation based on fossils and the chemical isotopes in sediments and corals. An increase of only 1.3°C would make the world warmer than at any time in the past 100,000 years. A warming trend would also alter the geographic distribution of precipitation, likely making agricultural areas of the central United States much drier, for example.

The ecosystems where the largest warming has *already* occurred are those in the far north, particularly northern coniferous forests and tundra. As snow and ice melt and uncover darker, more absorptive surfaces, these systems reflect less radiation back to the atmosphere and warm further. Arctic sea ice in the summer of 2007 covered the smallest area on record. Climate models suggest that there may be no summer ice there within a few decades, decreasing habitat for polar bears, seals, and seabirds. Higher temperatures also increase the likelihood of fires. In boreal forests of western North America and Russia, fires have burned twice the usual area in recent decades.

Range Shifts and Climate Change

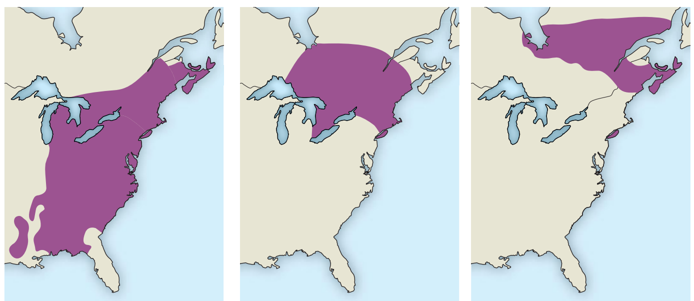
Many organisms, especially plants that cannot disperse rapidly over long distances, may not be able to survive the rapid climate change projected to result from global warming. Furthermore, many habitats today are more fragmented than ever (see Concept 43.3), further limiting the ability of many organisms to migrate.

One way to predict the possible effects of future climate change on geographic ranges is to look back at the changes that have occurred in temperate regions since the last ice age ended. Until about 16,000 years ago, continental glaciers covered much of North America and Eurasia. As the climate warmed and the glaciers retreated, tree distributions expanded northward. A detailed record of these changes is captured in fossil pollen deposited in lakes and ponds. (Recall from Chapter 26 that wind and animals sometimes disperse pollen and seeds over great distances.) If researchers can determine the climatic limits of current distributions of organisms, they can make predictions about how those distributions may change with continued climatic warming.

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

Will plants and other species be able to keep up with the much more rapid warming projected for this century? Ecologists have attempted to answer this question for the American beech (*Fagus grandifolia*). Their models predict that the northern limit of the beech's range may move 700–900 km northward in the next century, and its southern range limit will shift even more. The current and predicted geographic ranges of this species under two different climate-change scenarios are illustrated in **Figure 43.27**. If these predictions are even approximately correct, the beech's range must shift 7–9 km northward per year to keep pace with the warming climate. However, since the end of the last ice age, the beech has moved at a rate of only 0.2 km per year. Without human help in moving to new habitats, species such as the American beech may have much smaller ranges or even become extinct.

Changes in the distributions of species are already evident in many well-studied groups of terrestrial, marine, and freshwater organisms, consistent with the signature of a warmer world. In Europe, for instance, the northern range limits of



(a) Current range © 1989 AAAS | **(b) 4.5°C warming over next century** | **(c) 6.5°C warming over next century**

▲ **Figure 43.27 Current range and predicted range for the American beech under two climate-change scenarios.**

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

22 of 35 butterfly species studied had shifted farther north by 35–240 km over the time periods for which records exist, in some cases beginning in 1900. Other research shows that a Pacific diatom, *Neodenticula seminae*, recently has colonized the Atlantic Ocean for the first time in 800,000 years. As Arctic sea ice has receded in the past decade, the increased flow of water from the Pacific has swept these diatoms around Canada and into the Atlantic, where they quickly became established.

Climate Change Solutions

We will need a variety of approaches to slow global warming and climate change in general. Quick progress can be made by using energy more efficiently and by replacing fossil fuels with renewable solar and wind power and, more controversially, with nuclear power. Today, coal, gasoline, wood, and other organic fuels remain central to industrialized societies and cannot be burned without releasing CO_2. Stabilizing CO_2 emissions will require concerted international effort and changes in both personal lifestyles and industrial processes.

Another important approach to slowing global warming is to reduce deforestation around the world, particularly in the tropics. Deforestation currently accounts for about 12% of greenhouse gas emissions. Recent research shows that paying countries *not* to cut forests could decrease the rate of deforestation by half within 10 to 20 years. Reduced deforestation would not only slow the buildup of greenhouse gases in our atmosphere but sustain native forests and preserve biodiversity, a positive outcome for all.

CONCEPT CHECK 43.4

1. How can the addition of excess mineral nutrients to a lake threaten its fish population?
2. **MAKE CONNECTIONS** There are vast stores of organic matter in the soils of northern coniferous forests and tundra around the world. Suggest an explanation for why scientists who study global warming are closely monitoring these stores (see Figure 42.12).

For suggested answers, see Appendix A.

CONCEPT 43.5

The human population is no longer growing exponentially but is still increasing rapidly

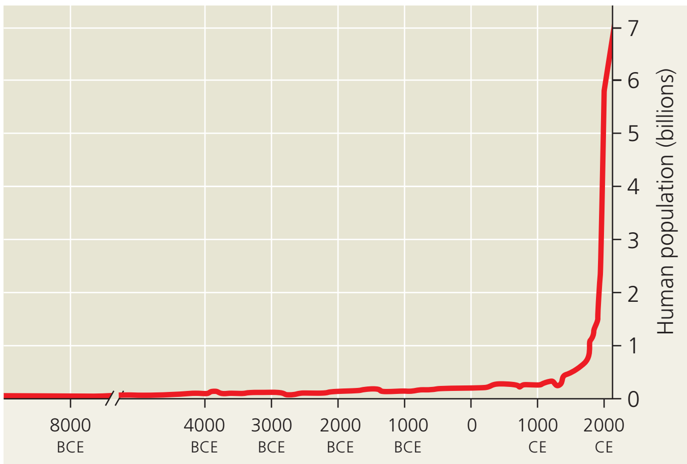
Global environmental problems, such as climate change, arise from the intersection of two factors. One is the growing amount of goods and resources that each of us consumes. The other is the increasing size of the human population, which has grown at an unprecedented rate in the last few centuries. No population can grow indefinitely, however. In this section, we'll apply ecological concepts to the specific case of the human population.

The Global Human Population

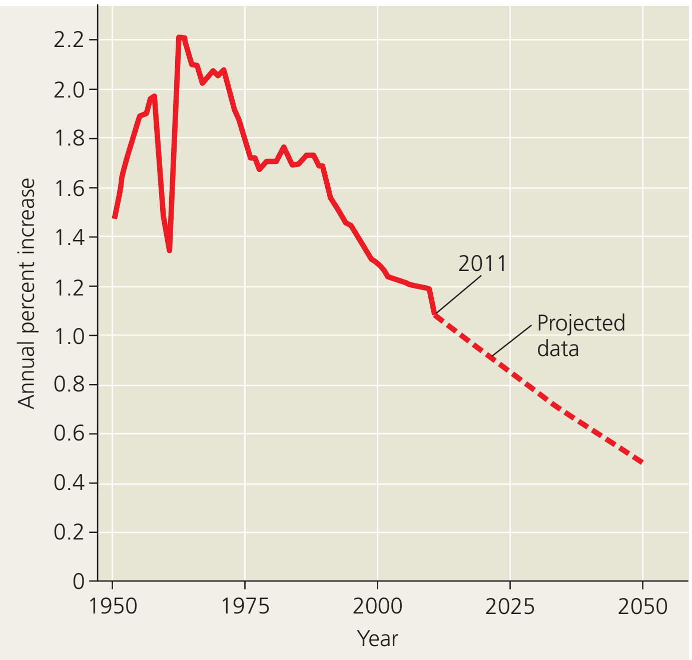
The exponential growth model (see Figure 40.19) approximates the human population explosion over the last four centuries **(Figure 43.28)**. Ours is a singular case; no other population of large animals has likely ever sustained so much growth for so long. The human population increased relatively slowly until about 1650, at which time approximately 500 million people inhabited Earth. Our population doubled to 1 billion within the next two centuries, doubled again to 2 billion by 1930, and doubled still again by 1975 to more than 4 billion. The global population is now more than 7 billion and is increasing by about 78 million each year. At this rate, it takes only about four years to add the equivalent of another United States to the world population. Ecologists predict a population of 8.1–10.6 billion people on Earth by the year 2050.

Though the global population is still growing, the *rate* of growth did begin to slow during the 1960s **(Figure 43.29)**. The annual rate of increase in the global population peaked at 2.2% in 1962 but had declined to 1.1% by 2011. Current models project a continued decline in the annual growth rate to roughly 0.5% by 2050, a rate that would still add 45 million more people per year if the population climbs to a projected 9 billion. The reduction in growth rate over the past four decades shows that the human population has departed from true exponential growth, which assumes a constant rate. This departure is the result of fundamental changes in population dynamics due to diseases, including AIDS, and to voluntary population control.

The growth rates of individual nations vary with their degree of industrialization. In industrialized nations, populations are



▲ **Figure 43.28 Human population growth (data as of 2011).** The global human population has grown almost continuously throughout history, but it skyrocketed after the Industrial Revolution. The rate of population growth has slowed in recent decades, mainly as a result of decreased birth rates throughout the world.



▲ **Figure 43.29 Annual percent increase in the global human population (data as of 2011).** The sharp dip in the 1960s is due mainly to a famine in China in which about 60 million people died.

near equilibrium, with growth rates of about 0.1% per year and reproductive rates near the replacement level (total fertility rate = 2.1 children per female). In countries such as Canada, Germany, Japan, and the United Kingdom, total reproductive rates are in fact *below* replacement. These populations will eventually decline if there is no immigration and if the birth rate does not change. In fact, the population is already declining in many eastern and central European countries.

In contrast, most of the current global population growth of 1.1% per year is concentrated in less industrialized nations, where about 80% of the world's people now live. Countries such as Afghanistan, Uganda, and Jordan had populations that grew by more than 3% *per year* between 2005 and 2010. Although death rates have declined rapidly since 1950 in many less industrialized countries, birth rates have declined substantially in only some of them. The fall in birth rate has been most dramatic in China. Largely because of the Chinese government's strict one-child policy, the expected total fertility rate (children per woman per lifetime) decreased from 5.9 in 1970 to 1.6 in 2011. The transition to lower birth rates has also been rapid in some African countries, though birth rates remain high in most of sub-Saharan Africa. In India, birth rates have fallen more slowly.

A unique feature of human population growth is our ability to control family sizes using family planning and voluntary contraception. Social change and the rising educational and career aspirations of women in many cultures encourage women to delay marriage and postpone reproduction. Delayed reproduction helps to decrease population growth rates and to move a society toward zero population growth under conditions of low birth rates and low death rates. However, there is a great deal of disagreement as to how much support should be provided for global family planning efforts.

Global Carrying Capacity

No ecological question is more important than the future size of the human population. The projected worldwide population size depends on assumptions about future changes in birth and death rates. As we noted earlier, population ecologists project a global population of approximately 8.1–10.6 billion people in 2050. In other words, without some catastrophe, an estimated 1–4 billion people will be added to the population in the next four decades because of the momentum of population growth. But just how many humans can the biosphere support? Will the world be overpopulated in 2050? Is it *already* overpopulated?

Estimates of Carrying Capacity

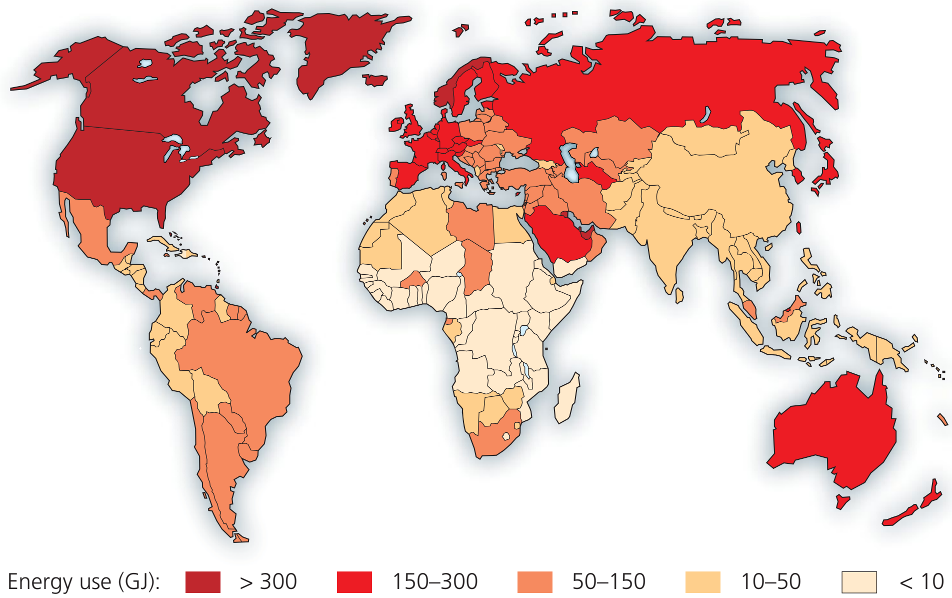
Estimates of the human carrying capacity of Earth have varied from less than 1 billion to more than 1,000 billion (1 trillion), with an average of 10–15 billion. Carrying capacity is difficult to estimate, and scientists use different methods to produce their estimates. Some current researchers use curves like that produced by the logistic equation (see Figure 40.19) to predict the future maximum of the human population. Others generalize from existing "maximum" population density and multiply this number by the area of habitable land. Still others base their estimates on a single limiting factor, such as food, and consider variables such as the amount of available farmland, the average yield of crops, the prevalent diet—vegetarian or meat based—and the number of calories needed per person per day.

Limits on Human Population Size

A more comprehensive approach to estimating the carrying capacity of Earth is to recognize that humans have multiple constraints: We need food, water, fuel, building materials, and other resources, such as clothing and transportation. The **ecological footprint** concept summarizes the aggregate land and water area required by each person, city, or nation to produce all the resources it consumes and to absorb all the waste it generates. One way to estimate the ecological footprint of the entire human population is to add up all the ecologically productive land on the planet and divide by the population. This calculation yields approximately 2 ha per person (1 ha = 2.47 acres). Reserving some land for parks and conservation means reducing this allotment to 1.7 ha per person—the benchmark for comparing actual ecological footprints. Anyone who consumes resources that require more than 1.7 ha to produce is said to be using an unsustainable share of Earth's resources. A typical ecological footprint for a person in the United States is about 10 ha.

Ecologists sometimes calculate ecological footprints using other currencies besides land area, such as energy use. Average energy use differs greatly in developed and developing nations (**Figure 43.30**). A typical person in the United States, Canada, or Norway consumes roughly 30 times the energy that a person in central Africa does. Moreover, fossil fuels, such as oil, coal, and natural gas, are the source of 80% or more of the energy used in most developed nations. This unsustainable reliance on fossil fuels is changing Earth's climate and increasing the amount of waste that each of us produces. Ultimately, the combination of resource use per person and population density determines our global ecological footprint.

How many people our planet can sustain depends on the quality of life each of us enjoys and the distribution of wealth across people and nations, topics of great concern and political debate. Unlike other organisms, we can decide whether zero population growth will be attained through social changes based on human choices or, instead, through increased mortality due to resource limitation, plagues, war, and environmental degradation.



▲ **Figure 43.30 Annual per capita energy use around the world.** A gigajoule (GJ) equals 10^9 J. For comparison, leaving a 100-watt light bulb on continuously for one year would use 3.15 GJ.

CONCEPT CHECK 43.5

1. How has the growth of Earth's human population changed in recent decades? Answer in terms of growth rate and the number of people added each year.
2. **WHAT IF?** What choices can you make to influence your own ecological footprint?

For suggested answers, see Appendix A.

CONCEPT 43.6

Sustainable development can improve human lives while conserving biodiversity

With the loss and fragmentation of habitats, changes in Earth's physical environment and climate, and increasing human population, we face difficult trade-offs in managing the world's resources. Preserving all habitat patches isn't feasible, so biologists must help societies set conservation priorities by identifying which habitat patches are most crucial. Ideally, implementing these priorities should also improve the quality of life for local people. Ecologists use the concept of *sustainability* as a tool to establish long-term conservation priorities.

Sustainable Development

We need to understand the interconnections of the biosphere if we are to protect species from extinction and improve the quality of human life. To this end, many nations, scientific societies, and other groups have embraced the concept of **sustainable development**, economic development that meets the needs of people today without limiting the ability of future generations to meet their needs.

Achieving sustainable development is an ambitious goal. To sustain ecosystem processes and stem the loss of biodiversity, we must connect life science with the social sciences, economics, and the humanities. We must also reassess our personal values. As you learned in Concept 43.5, those of us living in developed nations have a larger ecological footprint than do people living in developing nations. By including the long-term costs of consumption in profit-and-loss calculations, we can learn to value the natural processes that sustain us. The following case study illustrates how the combination of scientific and personal efforts can make a significant difference in creating a truly sustainable world.

Case Study: *Sustainable Development in Costa Rica*

The success of conservation in Costa Rica that we discussed in Concept 43.3 has required a partnership between the national government, nongovernment organizations (NGOs), and private citizens. Many nature reserves established by individuals have been recognized by the government as national wildlife reserves and given significant tax benefits. However, conservation and restoration of biodiversity make up only one facet of sustainable development; the other key facet is improving the human condition.

How have the living conditions of the Costa Rican people changed as the country has pursued its conservation goals? Two of the most fundamental indicators of living conditions are infant mortality rate and life expectancy. From 1930 to 2010, the infant mortality rate in Costa Rica declined from 170 to 9 per 1,000 live births; over the same period, life expectancy increased from about 43 years to 79 years. Another indicator of living conditions is the literacy rate, which was 96% in 2011, compared to 97% in the United States. Such statistics show that living conditions in Costa Rica have improved greatly over the period in which the country has dedicated itself to conservation and restoration. While this result does not prove that conservation *causes* an improvement in human welfare, we can say with certainty that development in Costa Rica has attended to both nature *and* people.

The Future of the Biosphere

Our modern lives are very different from those of early humans, who hunted and gathered to survive. Their reverence for the natural world is evident in the early murals of wildlife they painted on cave walls **(Figure 43.31a)** and in the stylized visions of life they sculpted from bone and ivory **(Figure 43.31b)**.

Our lives reflect remnants of our ancestral attachment to nature and the diversity of life—the concept of *biophilia* that was introduced early in this chapter. We evolved in natural environments rich in biodiversity, and we still have an affinity for such settings **(Figure 43.31c, d)**. E. O. Wilson makes the case that our biophilia is innate, an evolutionary product of natural selection acting on a brainy species whose survival depended on a close connection to the environment and a practical appreciation of plants and animals.

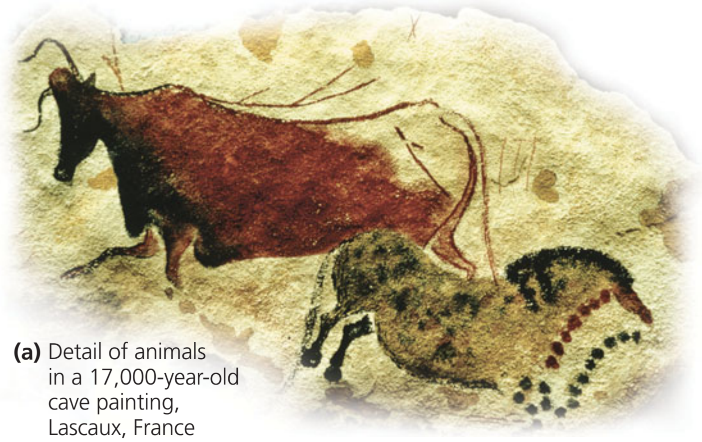
Our appreciation of life guides the field of biology today. We celebrate life by deciphering the genetic code that makes each species unique. We embrace life by using fossils and DNA to chronicle evolution through time. We preserve life through our efforts to classify and protect the millions of species on Earth. We respect life by using nature responsibly and reverently to improve human welfare.

Biology is the scientific expression of our desire to know nature. We are most likely to protect what we appreciate, and we are most likely to appreciate what we understand. By learning about the processes and diversity of life, we also become more aware of ourselves and our place in the biosphere. We hope this book has served you well in this lifelong adventure.

CONCEPT CHECK 43.6

1. What is meant by the term *sustainable development*?
2. How might biophilia inspire us to conserve species and restore ecosystems?
3. **WHAT IF?** Suppose a new fishery is discovered, and you are put in charge of developing it sustainably. What ecological data might you want on the fish population? What criteria would you apply for the fishery's development?

For suggested answers, see Appendix A.



(a) Detail of animals in a 17,000-year-old cave painting, Lascaux, France

(b) A 30,000-year-old ivory carving of a water bird, found in Germany

(c) Nature lovers on a wildlife-watching expedition

(d) A young biologist holding a songbird

▲ **Figure 43.31 Biophilia, past and present.**

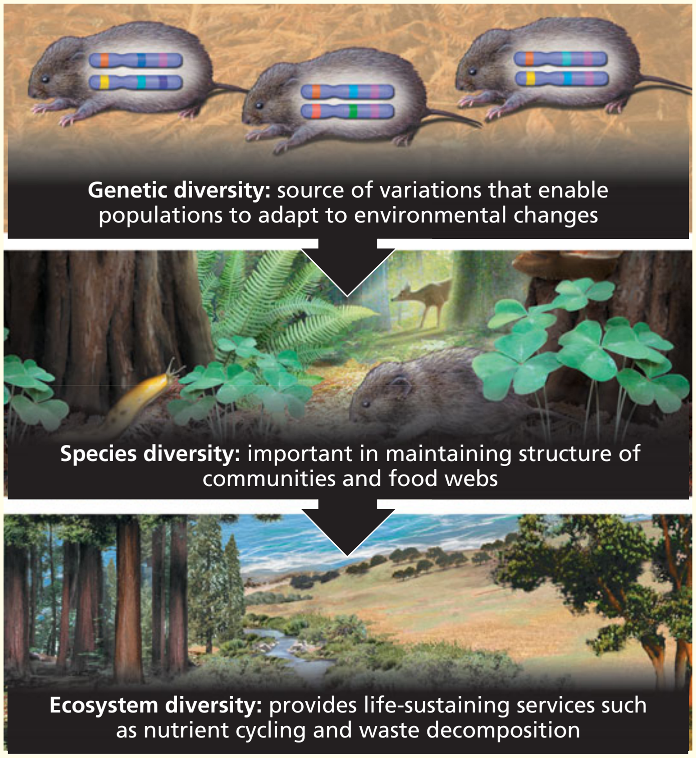
43 Chapter Review

SUMMARY OF KEY CONCEPTS

CONCEPT 43.1

Human activities threaten Earth's biodiversity (pp. 883–888)

- Biodiversity can be considered at three main levels:



- Our biophilia enables us to recognize the value of biodiversity for its own sake. Other species also provide humans with food, fiber, medicines, and **ecosystem services**.
- Four major threats to biodiversity are habitat loss, **introduced species**, overharvesting, and global change.

? *Give at least three examples of key ecosystem services that nature provides for people.*

CONCEPT 43.2

Population conservation focuses on population size, genetic diversity, and critical habitat (pp. 888–891)

- When a population drops below a **minimum viable population (MVP)** size, its loss of genetic variation due to nonrandom mating and genetic drift can trap it in an **extinction vortex**.
- The declining-population approach focuses on the environmental factors that cause decline, regardless of absolute population size. It follows a step-by-step conservation strategy.
- Conserving species often requires resolving conflicts between the habitat needs of **endangered species** and human demands.

? *Why is the minimum viable population size smaller for a population that is more genetically diverse than it is for a less genetically diverse population?*

CONCEPT 43.3

Landscape and regional conservation help sustain biodiversity (pp. 891–895)

- The structure of a landscape can strongly influence biodiversity. As habitat fragmentation increases and edges become more extensive, biodiversity tends to decrease. **Movement corridors** can promote dispersal and help sustain populations.
- **Biodiversity hot spots** are also hot spots of extinction and thus prime candidates for protection. Sustaining biodiversity in parks and reserves requires management to ensure that human activities in the surrounding landscape do not harm the protected habitats. The **zoned reserve** model recognizes that conservation efforts often involve working in landscapes that are greatly affected by human activity.

? *Give two examples that show how habitat fragmentation can harm species in the long term.*

CONCEPT 43.4

Earth is changing rapidly as a result of human actions (pp. 895–900)

- Agriculture removes plant nutrients from ecosystems, so large supplements are usually required. The nutrients in fertilizer can pollute groundwater and surface water, where they can stimulate excess algal growth (eutrophication).
- The release of toxic wastes has polluted the environment with harmful substances that often persist for long periods and become increasingly concentrated in successively higher trophic levels of food webs (**biological magnification**).
- Because of the burning of wood and fossil fuels and other human activities, the atmospheric concentration of CO_2 and other greenhouse gases has been steadily increasing. The ultimate effects include significant global warming and other changes in climate.

? *In the face of biological magnification of toxins, is it healthier to feed at a lower or higher trophic level? Explain.*

CONCEPT 43.5

The human population is no longer growing exponentially but is still increasing rapidly (pp. 900–902)

- Since about 1650, the global human population has grown exponentially, but within the last 50 years, the rate of growth has fallen by half. While some nations' populations are growing rapidly, those of others are stable or declining in size.
- The carrying capacity of Earth for humans is uncertain. **Ecological footprint** is the aggregate land and water area needed to produce all the resources a person or group of people consume and to absorb all of their wastes. It is one measure of how close we are to the carrying capacity of Earth. With a world population of more than 7 billion people, we are already using many resources in an unsustainable manner.

? *How are we humans different from other species in being able to "choose" a carrying capacity?*

CONCEPT 43.6

Sustainable development can improve human lives while conserving biodiversity (pp. 902–903)

- The goal of the Sustainable Biosphere Initiative is to acquire the ecological information needed for the development, management, and conservation of Earth's resources.
- Costa Rica's success in conserving tropical biodiversity has involved a partnership between the government, other organizations, and private citizens. Human living conditions in Costa Rica have improved along with ecological conservation.
- By learning about biological processes and the diversity of life, we become more aware of our close connection to the environment and the value of other organisms that share it.

? *Why is sustainability such an important goal for conservation biologists?*

TEST YOUR UNDERSTANDING

Level 1: Knowledge/Comprehension

1. One characteristic that distinguishes a population in an extinction vortex from most other populations is that
a. its habitat is fragmented.
b. it is a rare, top-level predator.
c. its effective population size is much lower than its total population size.
d. its genetic diversity is very low.
e. it is not well adapted to edge conditions.

2. The main cause of the increase in the amount of CO_2 in Earth's atmosphere over the past 150 years is
a. increased worldwide primary production.
b. increased worldwide standing crop.
c. an increase in the amount of infrared radiation absorbed by the atmosphere.
d. the burning of larger amounts of wood and fossil fuels.
e. additional respiration by the rapidly growing human population.

3. What is the single greatest threat to biodiversity?
a. overharvesting of commercially important species
b. introduced species that compete with native species
c. pollution of Earth's air, water, and soil
d. disruption of trophic relationships as more and more prey species become extinct
e. habitat alteration, fragmentation, and destruction

Level 2: Application/Analysis

4. Which of the following is a consequence of biological magnification?
a. Toxic chemicals in the environment pose greater risk to top-level predators than to primary consumers.
b. Populations of top-level predators are generally smaller than populations of primary consumers.
c. The biomass of producers in an ecosystem is generally higher than the biomass of primary consumers.
d. Only a small portion of the energy captured by producers is transferred to consumers.
e. The amount of biomass in the producer level of an ecosystem decreases if the producer turnover time increases.

5. Which of the following strategies would most rapidly increase the genetic diversity of a population in an extinction vortex?
a. Capture all remaining individuals in the population for captive breeding followed by reintroduction to the wild.
b. Establish a reserve that protects the population's habitat.
c. Introduce new individuals transported from other populations of the same species.
d. Sterilize the least fit individuals in the population.
e. Control populations of the endangered population's predators and competitors.

6. Of the following statements about protected areas that have been established to preserve biodiversity, which one is *not* correct?
a. About 25% of Earth's land area is now protected.
b. National parks are one of many types of protected areas.
c. Most protected areas are too small to protect species.
d. Management of a protected area should be coordinated with management of the land surrounding the area.
e. It is especially important to protect biodiversity hot spots.

Level 3: Synthesis/Evaluation

7. **DRAW IT** Using Figure 43.26 as a starting point, extend the *x*-axis to the year 2100. Then extend the CO_2 curve, assuming that the CO_2 concentration continues to rise as fast as it did from 1974 to 2011. What will be the approximate CO_2 concentration in 2100? What ecological factors and human decisions will influence the actual rise in CO_2 concentration? How might additional scientific data help societies predict this value?

8. **SCIENTIFIC INQUIRY**
DRAW IT Suppose that you are managing a forest reserve, and one of your goals is to protect local populations of woodland birds from parasitism by the brown-headed cowbird. You know that female cowbirds usually do not venture more than about 100 m into a forest and that nest parasitism is reduced when woodland birds nest away from forest edges. The reserve you manage extends about 6,000 m from east to west and 1,000 m from north to south. It is surrounded by a deforested pasture on the west, an agricultural field for 500 m in the southwest corner, and intact forest everywhere else. You must build a road, 10 m by 1,000 m, from the north to the south side of the reserve and construct a maintenance building that will take up 100 m^2 in the reserve. Draw a map of the reserve, showing where you would put the road and the building to minimize cowbird intrusion along edges. Explain your reasoning.

9. **FOCUS ON EVOLUTION**
One factor favoring rapid population growth by an introduced species is the absence of the predators, parasites, and pathogens that controlled its population in the region where it evolved. In a short essay (100–150 words), explain how evolution by natural selection would influence the rate at which native predators, parasites, and pathogens in a region of introduction attack an introduced species.

10. **FOCUS ON INTERACTIONS**
In a short essay (100–150 words), identify the factor or factors that you think may ultimately be most important in regulating the human population, and explain your reasoning.

For selected answers, see Appendix A.