2018-19 AP BIOLOGY SUMMER ASSIGNMENT

Read Ch. 52-56 (Ecology Unit) in the 9th edition of Campbell and Reese *Biology*. You will need to stop and pick this up from the bookroom **before** you leave for summer break.

Complete the accompanying Study Guide packet for Ch. 52-56. This is due the first day I see you in class **Thurs, August 16th**. The packet is worth 30 points (for completion not accuracy…this is to help you learn). If there is a question for which you need more room (such as a concept map) label the question, use a separate sheet, and attach to the end of this packet.

TIP: *READ* the book, and start the assignment early. Not only will this make completing the study guide easier, but you will retain the content. As you will learn this year, the brain stores information best when you learn information in short chunks over time... it's science!

We will spend the first several days of class going over the questions/reviewing material. *You will be given a test over the ecology chapters within the first six days of school.*

Email bdiehl@wscloud.org or text me (740) 649-5031 if you have any questions! ☺

Ms. Diehl

UNIT 8 Ecology

Chapter 52

An Introduction to Ecology and the Biosphere

Key Concepts

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

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

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

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

Framework

This chapter describes the scope of ecology, global climate patterns, the major terrestrial and aquatic biomes, and the factors that help determine the distribution of species.

Chapter Review

Ecology is the study of interactions of organisms with each other and with their environment. Although ecology had its foundation in the observation of nature, rigorous experimental designs are now commonly used to investigate complex ecological questions.

The **biosphere** includes all of Earth's ecosystems and landscapes. **Global ecology** is the study of the effect of regional energy and material exchanges on the distribution and functioning of organisms across the biosphere.

A **landscape** or seascape consists of several ecosystems in a region; **landscape ecology** is the study of the flow of energy, materials, and organisms across connecting ecosystems.

An **ecosystem** includes all the organisms in an area and the abiotic factors with which they interact, and **ecosystem ecology** addresses such topics as the flow of energy and chemical cycling.

A **community** includes the populations of different species in an area; **community ecology** looks at such interactions as predation and competition and how these interactions between species affect community structure.

Population ecology is concerned with the factors that affect the size of populations, which are groups of individuals of the same species occupying a particular area.

Organismal ecology, which may include the disciplines of behavioral, physiological, and evolutionary ecology, considers the responses and adaptations of an organism to its environment.

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

The **climate,** or prevailing weather conditions of an area, is influenced by temperature, precipitation, sunlight, and wind. **Macroclimate** is the climatic pattern over an entire region; **microclimate** is the small-scale variations within a particular habitat.

Global Climate Patterns The absorption of solar radiation heats the atmosphere, land, and water, setting patterns for temperature variations, air circulation, and water evaporation that cause latitudinal variations in climate. The shape of Earth and the tilting of its axis create seasonal variations in day length and temperature, which increase with latitude. The **tropics,** located between latitudes 23.5° north and 23.5° south, receive the greatest amount of and least variation in solar radiation.

The global circulation of air begins as intense solar radiation near the equator causes warm, moist air to rise and release its water, producing the characteristic wet tropical climate, the arid conditions around 30° north and south as dry air descends, the fairly wet though cool climate at about 60° latitude as air rises again, and the cold and rainless climates of the polar regions. Air flowing along Earth's surface produces global wind patterns, such as the cooling trade winds blowing from east to west in the tropics and the prevailing westerlies in temperate zones.

Regional and Local Effects on Climate The changing angle of the sun over the year produces wet and dry seasons around 20° north and 20° south latitude. Seasonal wind pattern changes affect ocean currents, sometimes causing upwellings of cold, nutrient-rich water.

Coastal areas are generally wetter than inland areas, and large bodies of water moderate the climate. Water warmed at the equator flows toward the North Atlantic and warms the coast of western Europe as the Gulf Stream. A *Mediterranean climate* is created when cool, dry ocean breezes warm as they cross land, absorbing moisture and creating a hot, rainless climate.

INTERACTIVE QUESTION 52.1

Describe how mountains affect local climate with respect to the following three factors:

a. sunlight

b. temperature

c. rainfall

Microclimate Climate also varies on a very small scale. Differences in **abiotic** features created by trees, open spaces, or even fallen logs or large stones affect the local distributions of organisms. **Biotic** factors, or living organisms, also influence the distribution and abundance of organisms.

Global Climate Change Scientists predict that increasing concentrations of CO_2 and other greenhouse gases will warm the Earth 1–6°C by the end of the twenty-first century. Such climate change will have great effects on the distributions of plants and animals. Fossil pollen deposits have documented the rates of northward expansion of the ranges of various tree species following the last continental glaciers. As their geographic limits change with climatic warming, seed dispersal may not be rapid enough for some species of plants to move into new suitable habitat as their former ranges become inhospitable. Changes in distribution have already been documented for many plant and animal groups.

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

Biomes are major types of ecosystems characterized by the predominant vegetation or (in aquatic biomes) by the physical environment.

Climate and Terrestrial Biomes A **climograph** plots annual mean temperature and rainfall for a region; generally these values correlate with the distribution of various biomes. Overlaps of biomes on a climograph indicate the importance of variation in the seasonal patterns of rainfall and temperature.

General Features of Terrestrial Biomes Biomes are usually named for their predominant vegetation and major climatic features. Each biome also has characteristic microorganisms, fungi, and animals. The area of transition between biomes is called an **ecotone**.

Terrestrial biomes have vertical stratification, such as the layers in a forest from upper canopy, low tree layer, shrub understory, herbaceous plant ground layer, forest floor (litter), to root layer. Vertical stratification of vegetation provides diverse habitats for animals.

Species composition of any one biome varies locally. Often, convergent evolution has produced a superficial resemblance of unrelated species.

Disturbance and Terrestrial Biomes A **disturbance** is an event such as a fire, a storm, or human activity that can modify a community and alter resource availability. The patchiness of most biomes results from disturbances. Grasslands, savannas, chaparral, and many coniferous forests are maintained by the periodic disturbance of fire. Urban and agricultural communities now cover a large portion of Earth's land mass.

Exploring Terrestrial Biomes Tropical forests occur in equatorial and subequatorial regions. Variations in rainfall result in **tropical dry forests**, where rainfall is seasonal, and **tropical rain forests**, where rainfall is more constant and abundant. Temperatures are uniformly high. The tropical rain forest has pronounced vertical stratification, including emergent trees above a closed canopy and abundant epiphytes. Animal diversity is higher than in any other terrestrial biome. Agriculture and development are destroying many tropical forests.

Characterized by low and variable precipitation, **deserts** occur around 30° north and south latitude and in the interior of continents. Deserts may be hot or cold, and temperature varies seasonally and daily. Plants may use C_4 and CAM photosynthesis and have reduced leaf surface area, feature different water storage adaptations, and produce protective spines and toxins. Desert animals have physiological and behavioral adaptations to dry conditions. Irrigated agriculture and urbanization are now common in deserts, reducing natural biodiversity.

Savannas are equatorial and subequatorial grasslands with scattered trees and long dry seasons. Fires are common, and the dominant grasses and forbs (small nonwoody plants) are fire-adapted, drought-tolerant, and able to withstand grazing. Large grazing mammals and their predators are common, although insects are the dominant herbivores. Cattle ranching and overhunting have reduced the large-mammal populations of savannas.

Chaparral, common along coastlines in midlatitude continents, has cool, rainy winters and hot, dry summers. The dominant vegetation—evergreen shrubs and small trees—is maintained by and adapted to periodic fires. The high plant diversity present also includes many grasses and herbs. Browsing animals and small mammals are common. Urbanization and agriculture have reduced areas of chaparral.

Temperate grasslands are maintained by fire, seasonal drought, and grazing by large mammals. Winters are generally cold and dry; summers are hot and wet. Soils are deep and fertile, and most North American grasslands have been converted to farmland.

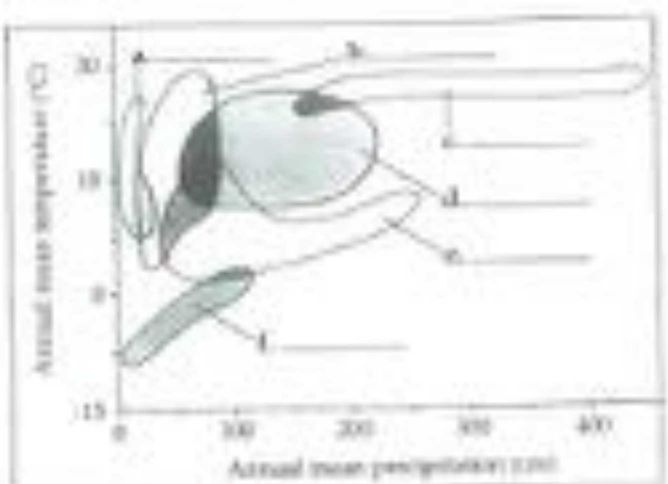
Characterized by broad-leaved deciduous trees, **temperate broadleaf forests** grow in midlatitude regions in the Northern Hemisphere, with smaller areas on other continents. Temperate broadleaf forests have distinct vertical layers. Winters are cold and summers hot and humid. During the cold winters, many mammals hibernate and birds migrate. Humans have heavily logged broadleaf forests, clearing land for agriculture and development.

The largest terrestrial biome, the **northern coniferous forest**, or taiga, is characterized by harsh winters with heavy snowfall and periodic droughts. Summers may be hot. Birds and large mammals are common animals. Old-growth stands of coniferous trees are rapidly being logged.

Tundra, covering large areas of the Arctic, is characterized by long, cold winters; short, cool summers; and dwarfed or matlike vegetation. A layer of frozen soil called permafrost restricts root growth. Migratory large mammals and birds are common. The alpine tundra, found at all latitudes on very high mountains, has similar plant communities. Mineral and oil extraction are becoming common in areas of arctic tundra.

INTERACTIVE QUESTION 52.2

Temperature and precipitation are two of the key factors that influence the vegetation found in a biome. On the following climograph, label the North American biomes (arctic and alpine tundra, northern coniferous forest, desert, temperate grassland, temperate broadleaf forest, and tropical forest) represented by each plotted area of temperature and precipitation.



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

One of the chemical differences in aquatic biomes is salt concentration—less than 0.1% for freshwater biomes versus an average of 3% for marine biomes. Three-fourths of Earth is covered by oceans, which influence global rainfall, climate, and wind patterns. Marine **algae and photosynthetic bacteria** produce a large portion of the world's O_2 and consume enormous amounts of CO_2. Freshwater biomes are influenced by the surrounding terrestrial biome.

Zonation in Aquatic Biomes Many aquatic biomes are layered both vertically and horizontally. The **photic zone** receives sufficient light for photosynthesis, whereas little light penetrates into the lower **aphotic zone.** The **pelagic zone** includes the waters of the photic and aphotic zone. The very deep ocean region is called the **abyssal zone.** The bottom substrate, called the **benthic zone,** is home to organisms collectively called **benthos.** Settling **detritus** (dead organic material) provides food for many benthic species.

In the ocean and in most lakes, a narrow layer of abrupt temperature change called a **thermocline** separates warmer surface waters from the cold bottom layer. In temperate lakes, seasonal temperature changes produce the **turnover** of water that sends oxygenated water to the bottom and brings nutrient-rich water to the surface.

Exploring Aquatic Biomes **Oligotrophic lakes** are often deep, nutrient poor, and generally oxygen rich. The nutrient-rich waters of **eutrophic lakes** may be seasonally depleted of oxygen in deeper regions due to decomposition. Rooted and floating plants are found in the **littoral zone** close to shore; phytoplankton and cyanobacteria inhabit the **limnetic zone.** Heterotrophs include floating zooplankton, benthic invertebrates, and fishes. Dumping of municipal wastes and runoff from fertilized lands can cause algal blooms, oxygen depletion, and fish kills.

Wetlands, defined as areas covered with water often enough to support plants adapted to water-saturated soil, are among the most productive of biomes. Water and soils may be periodically oxygen poor due to high rates of decomposition. Topography creates basin, riverine, and fringe wetlands. Wetlands filter nutrients and chemical pollutants and reduce flooding. Up to 90% of these richly diverse areas has been lost to draining and filling.

Streams and rivers are flowing habitats whose physical and chemical characteristics vary from the headwaters to the mouth. Oxygen levels are high in turbulently flowing water and low in murky, warm waters. Overhanging vegetation contributes to nutrient content. Diverse fishes and invertebrates inhabit the vertical zones of unpolluted rivers and streams. Human impact on streams and rivers includes pollution and damming.

Where a freshwater river meets the ocean, an estuary is formed. Salinity varies both spatially and daily with the rise and fall of tides. Salt marsh grasses and algae are the major producers. Estuaries serve as feeding and breeding areas for marine invertebrates, fish, and waterfowl. Pollution, filling, and dredging have extensively disrupted these highly productive biomes.

INTERACTIVE QUESTION 52.3

In the following table, indicate with a + or a − whether the listed biomes are relatively high or low in oxygen level, nutrient content, and productivity.

Biome	Oxygen Level	Nutrient Content	Productivity
Oligotrophic lake	a.		
Eutrophic lake	b.		
Headwater stream	c.		
Turbid river	d.		
Wetlands	e.		
Estuary	f.		

In **intertidal zones** the daily cycle of tides exposes the shoreline to variations in water, nutrients, and temperature, and to the mechanical force of wave action. Rocky intertidal communities are vertically stratified, with diverse marine algae and animals adapted to attaching firmly to the hard substrate. Sandy intertidal zones are home to burrowing worms, clams, and crustaceans. Oil pollutants have damaged many intertidal areas.

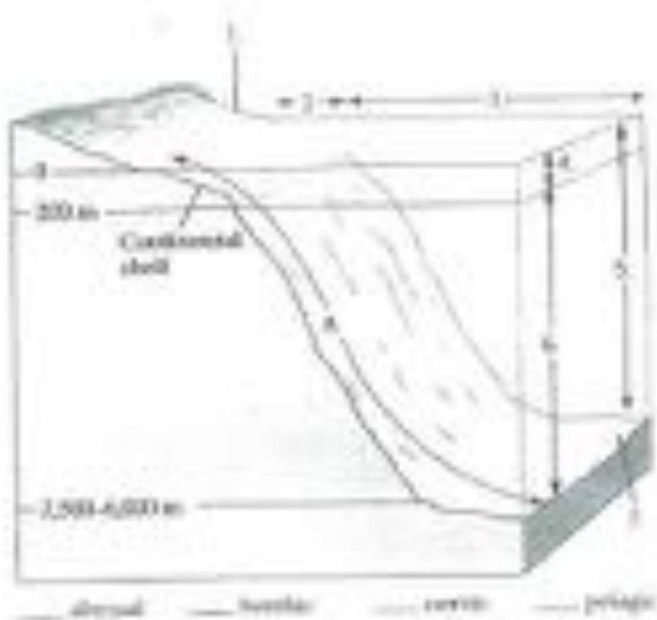
The water of the **oceanic pelagic biome** is typically nutrient poor but oxygen rich. Phytoplankton in the photic region are grazed on by numerous types of zooplankton. Free-swimming animals include squid, fishes, and marine mammals. Overfishing and waste dumping have damaged the Earth's oceans.

Found in the photic zone of clear tropical waters, coral reefs are highly diverse and productive biomes. The structure of the reef is produced by the calcium carbonate skeletons of the coral (various cnidarians) and serves as a substrate for red and green algae. The coral animals are nourished by symbiotic unicellular algae. Overfishing, coral collecting, pollution, and global warming are destroying coral reefs.

The **marine benthic zone** consists of the ocean floor. The shallow benthic areas of the **neritic zone** have diverse seaweeds and algae, as well as numerous invertebrates and fishes. The rest of the marine benthic zone receives no sunlight, and nutrients fall as detritus from the waters above. Inhabitants of the abyssal zone are adapted to cold and to high water pressure. Chemoautotrophic prokaryotes form the basis of a collection of organisms adapted to the hot, low-oxygen environment surrounding **deep-sea hydrothermal vents**. Overfishing has eliminated many benthic fish populations.

INTERACTIVE QUESTION 52.4

Different marine environments can be classified on the basis of light penetration, distance from shore, and open water vs. bottom. Match the following zones to their corresponding numbers on the diagram.



___ abyssal ___ benthic ___ neritic ___ pelagic

___ aphotic ___ intertidal ___ oceanic ___ photic

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

Interactions between organisms and their environments occur within ecological time. The cumulative effects of these interactions are seen in the adaptation of organisms to their environment over an *evolutionary time* frame. The distribution of species reflects these ecological and evolutionary interactions with both biotic and abiotic factors. Ecologists often work through a series of four logical questions to determine what factors limit the geographic distribution of a species.

Dispersal and Distribution **Dispersal** is the movement of individuals away from their original area. The cattle egret is an example of a species that has naturally extended its range through dispersal. Occasionally, such long-distance dispersal can lead to the adaptive radiation of many new species.

Transplants of a species can indicate whether dispersal limits its distribution. A successful transplant shows that the *potential range* of a species is larger than its *actual range*. Species that are introduced to new areas, either purposely or accidentally, often disrupt their new ecosystem.

Behavior and Habitat Selection Sometimes habitat selection behaviors keep organisms from occupying all of their potential range. Habitat selection by ovipositing insects, which often choose only certain plants, may limit the insects' distribution to the locations of their host plants.

Biotic Factors The distribution of a species may be limited by predation, disease, parasitism, competition, or lack of mutual symbionts. "Removal and addition" experiments test whether predators or herbivores limit the distribution of prey species or plants. Sea urchins were shown to limit the abundance and distribution of seaweeds.

Abiotic Factors A species' geographic distribution may be influenced by regional differences in abiotic factors.

Temperature is an important environmental factor because of its effects on metabolism. Most organisms function best within a narrow range of environmental temperatures.

The availability of water in different habitats can vary greatly. The distribution of organisms reflects their ability to obtain sufficient water and avoid desiccation in terrestrial habitats. Oxygen concentrations can be low in deep waters, in sediments rich in organic matter, and in flooded soils.

The ability of organisms to osmoregulate determines their distribution in freshwater, saltwater, or other high-salinity habitats.

Light energy drives almost all ecosystems. The quantity of sunlight is a limiting factor in aquatic environments and on forest floors. Excessive light intensity at high elevations and in deserts also limits the survival of plants and animals.

Soils, which vary in their physical structure, pH, and mineral composition, affect the distribution of plants and, in turn, the distribution of animals. Substrate composition in aquatic environments influences water chemistry and the types of organisms that can inhabit those areas.

INTERACTIVE QUESTION 52.5

List and give examples of the four factors that ecologists examine to understand the geographic distribution of a species.

a.

b.

c.

d.

Word Roots

a- = without; **bio-** = life (*abiotic*: nonliving; referring to physical and chemical properties of an environment)

abyss- = deep, bottomless (*abyssal zone*: the part of the ocean's benthic zone between 2,000 m and 6,000 m deep)

benthos- = the depths of the sea (*benthic zone*: the bottom surface of an aquatic environment)

estuar- = the sea (*estuary*: the area where a freshwater stream or river merges with the ocean)

eu- = good, well; **troph-** = food, nourishment (*eutrophic lake*: a lake with a high rate of productivity and nutrient cycling)

hydro- = water; **therm-** = heat (*deep-sea hydrothermal vent*: a dark, hot, oxygen-deficient environment associated with volcanic activity near the seafloor; the producer organisms are chemoautotrophic prokaryotes)

inter- = between (*intertidal zone*: the shallow zone of ocean adjacent to land and between the high- and low-tide lines)

limn- = a lake (*limnetic zone*: the well-lit, open surface waters of a lake far from shore)

litto- = the seashore (*littoral zone*: the shallow, well-lit waters of a lake close to shore)

micro- = small (*microclimate*: very fine-scale patterns of climate, such as the specific climatic conditions underneath a log)

oligo- = small, scant (*oligotrophic lake*: a nutrient-poor, clear lake with few phytoplankton)

pelag- = the sea (*pelagic zone*: the open-water component of aquatic biomes)

-photo = light (*aphotic zone*: the part of an ocean or lake beneath the photic zone, where light does not penetrate sufficiently for photosynthesis to occur)

thermo- = heat; **cline** = slope (*thermocline*: a narrow stratum of abrupt temperature change in the ocean and in many temperate-zone lakes)

Structure Your Knowledge

1. a. Define ecology.
   b. How does ecology relate to evolutionary biology?
2. a. What are biomes?
   b. What accounts for the similarities in life forms found in the same type of biome in geographically separated areas?

Test Your Knowledge

MULTIPLE CHOICE: *Choose the one best answer.*

1. Which level of ecology considers the effects of predation, parasitism, and competition on species distribution?
   a. landscape
   b. community
   c. ecosystem
   d. organismal
   e. population
2. Ecologists often use mathematical models and computer simulations because
   a. ecological experiments are always too broad in scope to be performed.
   b. most ecologists are mathematicians.
   c. ecology is becoming a more descriptive science.

d. these approaches allow ecologists to study the interactions of multiple variables and to simulate large-scale experiments.
e. variables can be manipulated with computers but cannot be manipulated in field experiments.

3. The ample rainfall of the tropics and the arid areas around 30° north and south latitudes are caused by
a. ocean currents that flow clockwise in the northern hemisphere and counterclockwise in the southern hemisphere.
b. the global circulation of air initiated by intense solar radiation near the equator that produces wet and warm air.
c. the tilting of Earth on its axis and the resulting seasonal changes in climate.
d. the heavier rain on the windward side of mountain ranges and the drier climate on the leeward side.
e. the location of tropical rain forests and deserts.

4. Which of the following statements reflects a concern about the effects of global climate change on tree species?
a. The increased ozone levels may damage leaf cells, reducing photosynthetic rates.
b. Trees may not be able to disperse fast enough to reach new habitats that meet their climatic requirements.
c. Warmer temperatures may speed tree growth, producing trees that are too tall and spindly.
d. The additional CO_2 in the atmosphere may actually increase photosynthetic rates and prove beneficial to tree growth.
e. All of the above are concerns.

5. Why do the tropics and the windward side of mountains receive more rainfall than areas around 30° latitude or the leeward side of mountains?
a. Rising air expands, cools, and drops its moisture.
b. Descending air condenses and drops its moisture.
c. The tropics and the windward side of mountains are closer to the ocean.
d. Solar radiation is greater in the tropics and on the windward side of mountains.
e. The rotation of Earth determines global wind patterns.

6. The permafrost of the arctic tundra
a. prevents plants from getting established and growing.
b. protects small animals during the long winters.
c. anchors plant roots in the frozen soil, helping them withstand the area's high winds.
d. prevents plant roots from penetrating deep into the soil.
e. Both b and c are correct.

7. Many plant species have adaptations for dealing with the periodic fires typical of a
a. savanna.
b. chaparral.
c. temperate grassland.
d. temperate broadleaf forest.
e. a, b, and c.

8. The best way to explain how two communities can have the same annual mean temperature and rainfall but very different biota and characteristics is that the communities
a. are found at different altitudes.
b. are composed of species that have very low dispersal rates.
c. are found on different continents.
d. receive different amounts of sunlight.
e. have different seasonal temperatures and patterns of rainfall throughout the year.

9. In which of the following biomes is sunlight most likely to be a limiting factor?
a. desert
b. estuary
c. ocean pelagic zone
d. grassland
e. coral reef

10. Which of the following aquatic zones is incorrectly paired with its description?
a. neritic zone—shallow region of ocean over the continental shelf
b. abyssal zone—very deep benthic region of the ocean
c. littoral zone—shallow waters close to shore in a lake
d. intertidal zone—shallow area of the ocean adjacent to land
e. pelagic zone—area of open water

11. In which of the following biomes would you expect to find organisms with adaptations for tolerating changes in salinity?
a. desert
b. wetland
c. deep-sea hydrothermal vent
d. estuary
e. intertidal zone

12. Phytoplankton are the basis of the food chain in
a. the headwaters of streams.
b. wetlands.
c. the oceanic photic zone.
d. rocky intertidal zones.
e. deep-sea hydrothermal vents.

13. Upwellings in oceans
    a. support reef communities.
    b. occur over deep-sea hydrothermal vents.
    c. are responsible for ocean currents.
    d. bring nutrient-rich water to the surface.
    e. are most common in tropical waters, where they bring oxygen-rich water to the surface.

14. Which of the following factors affect the distribution of a species?
    a. dispersal ability
    b. interactions with mutualistic symbionts
    c. climate and physical factors of the environment
    d. behavior, such as habitat selection
    e. All of the above factors influence where species are found.

15. An experiment that removed a species from an area would enable an ecologist to test
    a. whether moving the species to a new, varied habitat could lead to adaptive radiation.
    b. whether competition or predation from that species was limiting the local distribution of other species.
    c. whether dispersal ability was limiting the range of the species.
    d. whether abiotic factors were limiting the dispersal of the species.
    e. whether behavior or habitat selection had limited the distribution of the species.

MATCHING: *Match the biotic description with its biome.*

	Biome	Biotic Description
______	1. chaparral	A. broad-leaved deciduous trees
______	2. desert	B. lush growth, vertical layers
______	3. savanna	C. evergreen shrubs, fire-adapted vegetation
______	4. coniferous forest	D. scattered trees, grasses, and forbs
______	5. temperate broadleaf forest	E. tall stands of cone-bearing trees
______	6. temperate grassland	F. low shrubby or matlike vegetation, lichens
______	7. tropical rain forest	G. grasses adapted to fire and drought
______	8. tundra	H. widely scattered shrubs, cacti, and euphorbs

Chapter 53

Population Ecology

Key Concepts

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

53.2 The exponential model describes population growth in an idealized, unlimited environment

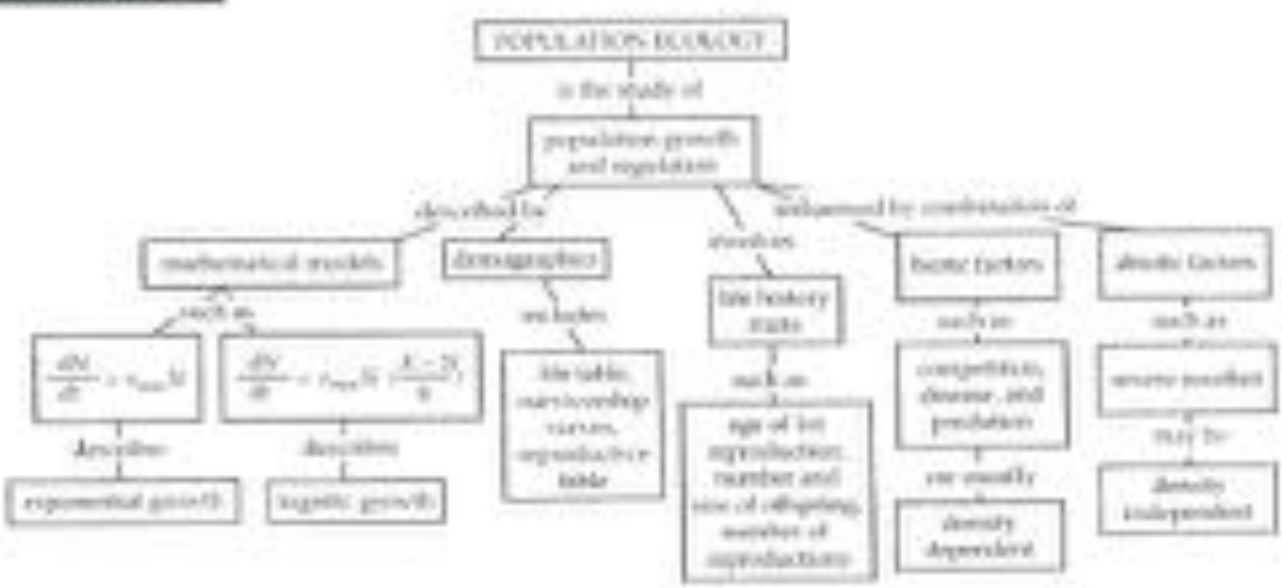
53.3 The logistic model describes how a population grows more slowly as it nears its carrying capacity

53.4 Life history traits are products of natural selection

53.5 Many factors that regulate population growth are density dependent

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

Framework



Chapter Review

Population ecology is the study of the influence of the abiotic and biotic environments on population size, density, and distribution.

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

A **population** is a localized group of individuals of the same species. Members of a population use the same resources and have a high probability of interacting and breeding with each other. Populations may be described by their size and geographic boundaries; ecologists define such boundaries based on the type of organism and the research question being asked.

Density and Dispersion The number of individuals per unit area or volume is a population's **density**; the pattern of spacing of these individuals is referred to as **dispersion**.

Scientists often use one of a variety of sampling techniques to estimate population density. Indirect indicators, such as burrows or nests, also may be used. In the **mark-recapture method**, a population is sampled twice. First, animals are trapped and marked (or identified), and released. Animals are then captured or sampled again. The proportion of the total second trapping that is marked indicates the proportion of the total population that was initially marked. The calculation uses the equation $x/n = s/N$ (where x is recaptured marked animals; n is number in second sampling; s is the number of animals initially marked and released; and N is estimated population size). Solving for $N = sn/x$.

INTERACTIVE QUESTION 53.1

In a mark-recapture study, an ecologist traps, marks, and releases 25 voles in a small wooded area. A week later she resets her traps and captures 30 voles, 10 of which are marked. What is her estimate of the vole population in that area?

Changes in population density reflect both additions of members through birth (including all forms of reproduction) and **immigration**, and removal of members through death and **emigration**.

Individuals may be dispersed in the population's geographic range in several patterns. *Clumping* may indicate a heterogeneous environment or social interactions between individuals.

Uniform distribution may be related to competition for resources and result from interactions between individuals. **Territoriality**, the defense of a bounded physical space, can lead to uniform dispersion. *Random spacing*, indicating the absence of strong interactions among individuals or a fairly uniform habitat, is less common.

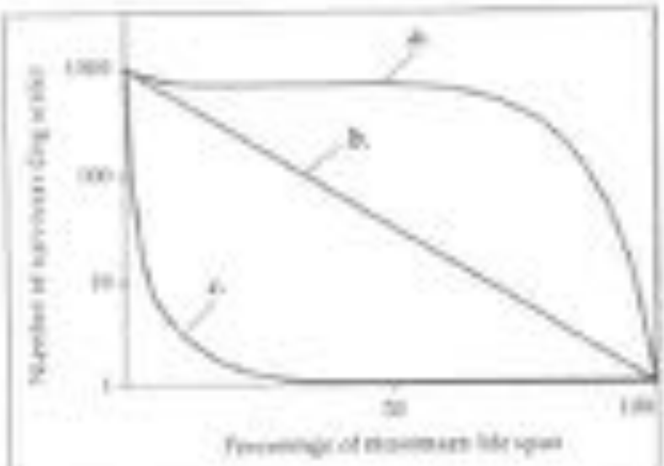
Demographics The study of the vital statistics of a population, such as birth and death rates, is called **demography**.

A **life table** presents age-specific survival data for a population. It can be constructed by following a **cohort** of organisms from birth to death and calculating the proportion of the cohort surviving in each age group.

A **survivorship curve** shows the number or proportion of members of a cohort still alive at each age. Survivorship curves are often based on a convenient beginning cohort of 1,000 individuals and typically use a logarithmic scale on the y-axis and a relative scale on the x-axis, so that species with different life spans can be compared on the same graph. There are three general types of survivorship curves. Type I has low mortality during early and middle age and a rapid increase with old age. In a Type II curve, death rate is relatively constant throughout the life span. A Type III curve has high initial mortality, with the few offspring that survive likely to reach adulthood. Many species show intermediate or more complex survivorship patterns.

INTERACTIVE QUESTION 53.2

Identify the types of survivorship curves in the following graph. For each type of curve, describe the characteristics of representative species and then cite some examples of those species.



In sexually reproducing species, demographers usually follow only the reproduction of females through the generations. A **reproductive table**, or fertility schedule, gives the age-specific reproductive rates in a population.

53.2 The exponential model describes population growth in an idealized, unlimited environment

Per Capita Rate of Increase A small population in a very favorable environment may exhibit unrestricted growth. Ignoring immigration and emigration, the change in population size during a specific time period is equal to the number of births minus the number of deaths.

Births and deaths can be expressed in terms of the average number per individual during a time period—that is, as a *per capita birth rate* (b) and a *per capita death rate* (m, for mortality). These rates can be calculated from estimates of population size (N) and from data in life tables and reproductive tables. The population growth equation using per capita birth and death rates becomes $\Delta N/\Delta t = bN - mN$. The per capita rate of increase (r) is the difference between the per capita birth and death rates, $r = b - m$. Zero population growth (ZPG) occurs when $r = 0$. The equation describing the change in the population at a particular instant in time uses differential calculus and is written as $dN/dt = r_{inst}N$.

Exponential Growth Under ideal conditions, a population may exhibit **exponential population growth**, or geometric population growth. Expressed as $dN/dt = r_{max}N$, exponential population growth produces a J-shaped growth curve when graphed. The larger the population (N) becomes, the faster the population grows. Periods of exponential growth may occur in some populations that exploit an unfilled environment or rebound from a catastrophic event.

INTERACTIVE QUESTION 53.3

Define r_{max}.

53.3 The logistic model describes how a population grows more slowly as it nears its carrying capacity

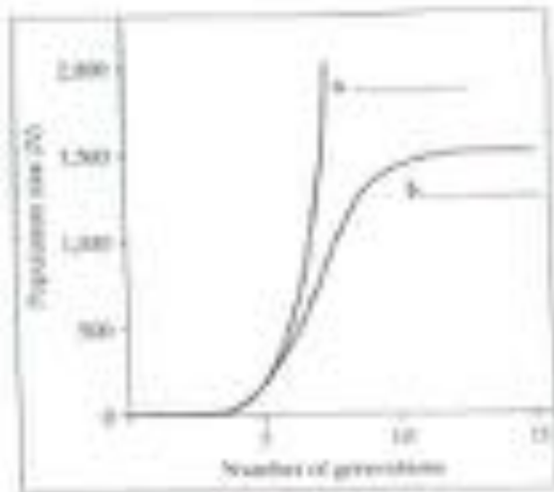
A population may grow exponentially for only a short time before its increased density limits the resources available to its members. The **carrying capacity** (K) is the maximum population size that a particular environment can support. Crowding and resource limitations may lead to decreased per capita birth rates and increased per capita death rates.

The Logistic Growth Model The per capita rate of increase decreases from its maximum at low population size to zero as carrying capacity is reached. The mathematical model of **logistic population growth** is $dN/dt = r_{max}N(K - N)/K$. The equation includes the expression $(K - N)/K$ to reflect the impact of increasing N on the per capita rate of increase as the population approaches the carrying capacity.

When N is small, $(K - N)/K$ is close to 1, and growth is approximately exponential ($r_{max}N$). As population size approaches the carrying capacity, the $(K - N)/K$ term becomes a smaller fraction, and per capita rate of increase is small. When N reaches K, the term $(K - N)/K$ is 0, and the population stops growing. The logistic model produces an S-shaped growth curve, and maximum increase in population numbers occurs when N is intermediate in size.

INTERACTIVE QUESTION 53.4

Label the following exponential and logistic growth curves, and write the equation associated with each curve. What is K for the population shown in curve *b*?



The Logistic Model and Real Populations Some laboratory populations of small animals and microorganisms show logistic growth. Natural populations often fluctuate around carrying capacity.

The logistic model makes the assumption that any increase in population size will have a negative effect on population growth. The *Allee effect* is seen in some populations, however, when individuals have a harder time reproducing if the population size is too small.

53.4 Life history traits are products of natural selection

The **life history** of an organism from birth through reproduction to death reflects evolutionary tradeoffs between survival and reproduction. Life history traits include the age at first reproduction, how often an organism reproduces, and the number of offspring produced in each reproductive episode.

Evolution and Life History Diversity Some species put all their reproductive resources into a single effort, called **semelparity**, or big-bang reproduction. Other species follow the strategy of **iteroparity**, making repeated reproductive efforts over a span of time. Two factors thought to be important in the selection for and evolution of these two reproductive strategies are the survival rate of young offspring and the probability that an adult will survive to reproduce more than once.

"Trade-offs" and Life Histories Because organisms have a finite energy budget, they cannot maximize all life history traits simultaneously. The costs of reproduction often include a reduction in survival. The production of large numbers of offspring is related to the selective pressures of high mortality rates of offspring in uncertain environments or from intense predation. Parental investments in the physical size of offspring (or seeds) and extended care increase the survival chances of offspring.

Natural selection will favor different life history traits at different population densities. Populations at high density, close to their carrying capacity, may experience **K-selection** or density-dependent selection for traits such as competitive ability and efficient resource use. In environments in which population density is low, **r-selection** (or density-independent selection) would favor traits that maximize population growth, such as the production of numerous, small offspring.

INTERACTIVE QUESTION 53.5

a. Explain why the life history of an organism cannot be to reproduce early and often, to have large numbers of offspring at a time, and to live a long life.

b. Indicate whether the following life history traits would be considered to be *r*-selected or *K*-selected:

early age at first reproduction; many small offspring produced

few, relatively large offspring produced every year

53.5 Many factors that regulate population growth are density dependent

Population Change and Population Density A birth rate or a death rate that does not change as population density changes is said to be **density independent**. The death rate is **density dependent** if it rises with increasing population density; the birth rate is density dependent if it falls with increasing population density. An equilibrium density may be reached in a population as long as birth rate or death rate or both are density dependent.

Mechanisms of Density-Dependent Population Regulation Density-dependent decreases in birth rate and increases in death rate may regulate populations through negative feedback.

Competition for resources such as nutrients or food may limit reproductive output. The availability of territorial space may be the limiting resource for some animals. Increased population densities may affect the transmission rate of diseases in both plant and animal populations. Predation may be a density-dependent factor when a predator feeds preferentially on a prey population that has reached a high density. The accumulation of toxic metabolic wastes may also be a limiting factor for some organisms.

Intrinsic factors may also regulate population size. Studies of mice have shown that even when food or shelter is not limiting, aggressive interactions and hormonal changes inhibit reproduction and increase mortality.

Population Dynamics All populations show fluctuations in numbers. **Population dynamics** is the study of these variations in population size and the biotic and abiotic factors that cause them. Fluctuations in populations of some large mammals, such as Soay sheep and moose on Isle Royale, may be linked to the severity of winter, the availability of food, or predation.

The 10-year cycles in the densities of snowshoe hares and lynx in northern forests have been studied to determine whether winter food shortages, predator overexploitation, or sunspot activity causes the cyclic collapses in hare populations. The decrease in ozone and increase in UV radiation associated with low sunspot activity result in plants producing more sunscreen chemicals and fewer herbivore-discouraging chemicals. Experimentally increasing the food supply raised the carrying capacity for hares, but the density cycles continued to occur in both experimental and control areas. Field ecologists determined that 90% of hare deaths are due to predation. Experiments that excluded predators from one area, and both excluded predators and added food to another area, support the hypothesis that it is mainly excessive predation that drives hare cycles, but available winter food supply is a contributing influence. Population peaks followed low sunspot activity, suggesting that sunspot activity also regulates hare populations.

Predator cycles most likely follow the population cycles of their prey, and these cycles may be accentuated when predators begin preying on one another when their usual prey becomes scarce.

Emigration may increase with population density. The aggregation of single-celled amoebas into a multicellular slug improved the ability of these protists to reach new food sources.

A group of populations occupying separated suitable habitats may be linked through immigration and emigration to form a **metapopulation**. Emigrants may serve to repopulate habitats in which local populations become extinct.

INTERACTIVE QUESTION 53.6

a. List some density-dependent factors that may limit population growth.

b. List some abiotic factors that may cause population fluctuations.

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

The Global Human Population After 1650, it took 200 years for the global population to double to 1 billion. In the next 80 years, it doubled to 2 billion; it doubled again to 4 billion in the next 45 years; and now, some 35 years later, it is more than 6.8 billion. The rate of growth has begun to slow, partly due to diseases such as AIDS and voluntary population control, although population ecologists project a population of 7.8–10.8 billion by 2050.

Population stability can be reached in one of two ways: ZPG = high birth rates – high death rates, or low birth rates – low death rates. The movement from the first configuration to the second is called the **demographic transition**. Death rates declined rapidly in most developing countries after 1950, but birth rate decline has been more uneven—from rapid in China to slower in sub-Saharan Africa and India. The world's annual population growth rate is regionally variable: it is near equilibrium (0.1%) in industrialized nations, with reproductive rate below the replacement level of 2.1 children per female in some countries. Less industrialized countries, where 80% of the world's population lives, contribute the most to the global growth rate of 1.2%.

Human population growth is unique in that it can be consciously controlled by voluntary contraception and family planning. The key to the demographic transition is reduced family size. In many cultures, women are receiving more education and delaying marriage and reproduction, thus slowing population growth.

The **age structure** of a population affects present and future growth and can be predictive of future social conditions and needs.

Infant mortality and life expectancy at birth vary among human populations, with mortality being much higher and life expectancy lower in less industrialized countries.

INTERACTIVE QUESTION 53.7

What do the age structure pyramids in Figure 53.24 predict for the future population growth of Afghanistan and Italy?

Global Carrying Capacity Estimates of Earth's carrying capacity have varied greatly and have averaged about 10–15 billion. These estimates involve different assumptions, such as the logistic equation, the amount of habitable land, or food as the limiting factor.

The concept of an **ecological footprint** takes into account multiple human needs and the land and water area required to meet those needs and absorb wastes. The amount of ecologically productive land area per person on Earth is estimated to be about 2 hectares (ha). Land for parks and conservation reduces this estimate to 1.7 ha per person. In the United States, a typical person, with an ecological footprint of about 10 ha, is using an unsustainable share of Earth's resources.

Ecological footprints may also be based on the amount of energy used. A typical person in the United States consumes roughly 30 times the energy consumed by an individual in central Africa.

The ultimate carrying capacity of Earth may be determined by food and water supplies, the availability of space or nonrenewable resources, degradation of the environment, or several interacting factors. When and how we reach zero population growth is an issue of great social and ecological consequence.

Word Roots

co- = together (*cohort*: a group of individuals of the same age in a population)

demo- = people; **-graphy** = writing (*demography*: the study of statistics relating to births and deaths in populations)

itero- = to repeat; **-parity** = to beget (*iteroparity*: type of reproduction in which adults produce offspring over many years; also known as repeated reproduction)

semel- = once (*semelparity*: type of reproduction in which an organism produces all of its offspring in a single event; also known as big-bang reproduction)

Structure Your Knowledge

1. Create a concept map to organize your understanding of the exponential and logistic equations—the mathematical models of population growth.
2. What is the best collection of life history traits that would maximize reproductive success?

Test Your Knowledge

MULTIPLE CHOICE: *Choose the one best answer.*

1. In an area with a heterogeneous distribution of suitable habitats, the dispersion pattern of a population is probably
   a. clumped.
   b. uniform.
   c. random.
   d. unpredictable.
   e. dense.
2. Which of the following statements about life tables is *not* true?
   a. They were first used by life insurance companies to estimate survival patterns.
   b. They show the age-specific death rate for a population.
   c. They are used to predict logistic growth.
   d. They can be used to construct survivorship curves.
   e. They are often constructed by following a cohort from birth to death.
3. A Type I survivorship curve is level at first, with a rapid increase in mortality in old age. This type of curve is
   a. typical of many invertebrates that produce large numbers of offspring.
   b. typical of humans and other large mammals.
   c. found most often in *r*-selected populations.
   d. almost never found in nature.
   e. typical of most species of birds.
4. The middle of the S-shaped growth curve in the logistic growth model
   a. shows that at middle densities, individuals of a population do not affect each other.
   b. is best described by the term *rN*.
   c. is the point where population growth begins to slow due to the Allee effect.
   d. is the period when competition for resources is the highest.
   e. is the period when the population growth rate is the highest.
5. The term $(K - N)/K$
   a. is the carrying capacity for a population.
   b. is greatest when K is very large.
   c. is zero when population size equals carrying capacity.
   d. increases in value as *N* approaches *K*.
   e. accounts for the overshoot of carrying capacity.
6. The carrying capacity for a population is estimated at 500, the population size is currently 400, and r_{max} is 0.1. What is dN/dt?
   a. 0.01
   b. 0.8
   c. 8
   d. 40
   e. 50
7. In order to maintain the largest sustainable fish harvest, fishing efforts should
   a. take only postreproductive fish.
   b. maintain the population close to its carrying capacity.
   c. reduce the population to a very low number to take advantage of exponential growth.
   d. maintain the population density close to ½ K.
   e. be prohibited.
8. Immigration and emigration are likely to play a role in population dynamics in
   a. metapopulations.
   b. exponential growth.
   c. demographic transition.
   d. big-bang reproduction.
   e. territoriality.
9. In a population in which offspring survival is quite low and the environment is inconsistent, one might expect
   a. the production of a small number of large offspring.
   b. the production of a large number of large offspring.
   c. iteroparity or repeated reproduction with a small number of offspring.
   d. semelparity.
   e. more *K*-selected traits.
10. Which of the following factors is *not* a density-dependent factor limiting a population's growth?
   a. increased specialization by a predator
   b. a limited number of available nesting sites
   c. a stress syndrome that alters hormone levels
   d. a very early fall frost
   e. intraspecific competition

11. A few members of a population have reached a favorable habitat containing few predators and unlimited resources, but their population growth rate is slower than that of the parent population. A possible explanation for this is that
   a. the genetic makeup of these founders may be less favorable than that of the parent population.
   b. the parent population may still be in the exponential part of its growth curve and not yet limited by density-dependent factors.
   c. the Allee effect may be operating; there are not enough population members present for successful survival and reproduction.
   d. a density-independent factor such as a severe storm has limited their growth.
   e. all of the above may apply.

In questions 12–16, use the following choices to indicate how these factors would be affected by the described changes.
   a. an increase
   b. a decrease
   c. no change
   d. the effect cannot be predicted

12. For a population regulated by density-dependent factors, what change would occur in clutch size or seed crop size with increased population density?

13. In the study of European kestrels described in the textbook (Figure 53.13), what effect did reducing the brood size by transferring chicks have on the survivorship of the parents in the following winter?

14. In a population showing exponential growth, what change would occur in dN/dt with an increase in N?

15. As a population approaches zero population growth, what change would occur in the per capita rate of increase (r)?

16. For an r-selected population regulated primarily by density-independent factors, what change would occur in the population growth rate if the carrying capacity of its environment were increased?

17. Experimental studies of the population cycles of the snowshoe hare and the lynx have shown that
   a. the hare population is regulated by its food resources because adding food increased the carrying capacity of experimental areas.
   b. hares are as likely to die of starvation as of predation.
   c. lynx are the only predators of hares, and that increases in the lynx population cause the cycles in the hare population.
   d. the stress of overcrowding causes the population cycles in both hare and lynx.
   e. the hare population is regulated by a combination of predators (not just the lynx) and by the effect of [illegible] activity on food quality; the lynx population appears to cycle in response to the availability of its prey.

18. The human population is growing at such a fast rate because
   a. the age structure of many countries is highly skewed toward younger ages.
   b. the death rate has greatly decreased since the Industrial Revolution.
   c. technology has increased Earth's carrying capacity.
   d. fertility rates in many developing countries are above the 2.1 children per female replacement level.
   e. all of the above are true.

19. The demographic transition is the gradual shift from
   a. a Type III survivorship curve to a Type I curve.
   b. iteroparity to semelparity.
   c. an age structure skewed toward the younger ages to an even age distribution.
   d. high birth rates and high death rates to low birth rates and low death rates.
   e. exponential growth to logistic growth.

20. An ecological footprint is an estimate of
   a. the carrying capacity of a nation.
   b. the number of offspring an adult produces and the resulting demand on resources.
   c. the land and water area needed per person to meet the current demand on resources.
   d. the size of a population in relationship to the resources it uses.
   e. how much energy is used to produce food for a vegetarian versus a meat eater.

Chapter 54

Community Ecology

Key Concepts

54.1 Community interactions are classified by whether they help, harm, or have no effect on the species involved

54.2 Diversity and trophic structure characterize biological communities

54.3 Disturbance influences species diversity and composition

54.4 Biogeographic factors affect community diversity

54.5 Pathogens alter community structure locally and globally

Framework

Communities are composed of populations of various species that may interact through competition, predation, herbivory, symbiosis, or facilitation. The structure of a community—its species composition and relative abundance—is determined by these interactions between species. Disturbances keep most communities in a state of nonequilibrium. Species diversity relates to community size and geographic location. Identifying the hosts and vectors of pathogens helps to combat zoonotic diseases.

Chapter Review

The collection of populations of different species living close enough to interact is called a biological **community**. Community ecologists study the interactions between species and the factors involved in determining a community's structure—the composition and the relative abundance of its species.

54.1 Community interactions are classified by whether they help, harm, or have no effect on the species involved

Interspecific interactions occur between the different species living in a community. The positive or negative effect of these interactions on the survival and reproduction of a population can be signified by + or − signs.

Competition If populations of two species use the same limited resource, **interspecific competition** may negatively affect one or both populations.

G. F. Gause's laboratory experiments showed that two species of *Paramecium* that rely on the same limited resource could not coexist in the same community. The **competitive exclusion** principle predicts that the less efficient competitor will be eliminated locally.

An organism's **ecological niche** is described as its role in an ecosystem—its use of biotic and abiotic resources. The competitive exclusion principle holds that two species with identical niches cannot coexist permanently in a community.

Resource partitioning, slight variations in niche that allow ecologically similar species to coexist, provides indirect evidence that competition was a selection factor in the evolution of a species' niche. Due to competition, a species' *realized niche* might be smaller than its *fundamental niche*. **Character displacement** of some morphological trait or in resource use enables closely related sympatric species to avoid competition. When these species are allopatric (geographically separated), their differences may be much smaller.

INTERACTIVE QUESTION 54.1

Whenever these two mouse species coexist, *Acomys cahirinus* is nocturnal, whereas *A. russatus* is active during the day. When all *A. cahirinus* were removed from a research site, diurnal *A. russatus* mice became nocturnal. How were resources partitioned between these species when they coexisted, and what do these results indicate about the niche of *A. russatus*?

Predation **Predation** involves a predator killing and eating prey. Predator adaptations include acute senses, speed and agility, camouflage coloration, and physical structures such as claws, fangs, teeth, and stingers.

Animals can defend against predation by hiding, fleeing, or forming herds or schools. Potential prey may use camouflage in the form of **cryptic coloration**. Mechanical and chemical defenses discourage predation. Some animals passively accumulate toxic compounds from the food they eat; others may synthesize their own toxins. Bright, conspicuous, **aposematic coloration** in prey species "warns" predators that the prey possesses chemical defenses.

Prey may use mimicry to exploit the warning coloration of other species. Predators may use mimicry to "bait" their prey.

INTERACTIVE QUESTION 54.2

Name the type of mimicry described in each of the following descriptions:

a. harmless species resembling a poisonous or distasteful species

b. mutual imitation by two or more unpalatable species

Herbivory In **herbivory**, an herbivore eats parts of a plant or alga. Most herbivores are small invertebrates such as insects, which may have chemical sensors that recognize nontoxic and nutritious plants. Herbivores may have teeth or digestive systems adapted for processing vegetation.

Plants may defend themselves with mechanical devices, such as thorns, or chemical compounds. Distasteful or toxic chemicals include such well-known compounds as strychnine, nicotine, tannins, and various spices.

Symbiosis Symbiosis may be defined as the relationship between organisms of two species that live in direct contact.

In **parasitism**, a parasite obtains its nourishment from its **host**. Parasites that live within a host are called **endoparasites**; those that feed on the surface of a host are called **ectoparasites**. Parasitoid insects lay eggs on or in hosts, on which their larvae then feed.

Parasites may have complex life cycles with a number of hosts. Parasites can have a substantial effect on the density of their host population.

In **mutualism**, interactions between species benefit both participants. In obligate mutualism, at least one species is unable to survive on its own; in facultative mutualism, both species can survive alone. Mutualistic interactions may involve the coevolution of related adaptations in both species.

In **commensalism**, only one member appears to benefit from the interaction. Examples include "hitchhiking" species and species that feed on food incidentally exposed by another species.

Facilitation In **facilitation**, a species positively affects the survival and reproduction of other species without the intimate association of symbiosis. This type of interaction is common in plant ecology, in which one plant species improves the soil in ways that benefit other species.

INTERACTIVE QUESTION 54.3

Name and give examples of the interspecific interactions symbolized in the table.

	Interspecific Interaction	Examples
−/−	a.	
+/+	b.	
+/0	c.	
+/−	d.	
+/−	e.	
+/−	f.	
+/+ or 0/+	g.	

54.2 Diversity and trophic structure characterize biological communities

Species Diversity The species diversity of a community is determined both by species richness, the number of different species present, and by relative abundance, the proportional abundance of the different species.

A widely used quantitative diversity index is **Shannon diversity** (H), which is based on species richness and relative abundance:

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

where p is the proportion of each species (A, B, C, and so on) in the community, and ln is the *natural log*. Thus Shannon diversity (H) for a community is the negative sum of $p \ln p$ for all species present.

INTERACTIVE QUESTION 54.4

Tide pool 1 has three species of sea urchins with the following numbers: A = 5, B = 5, C = 5; tide pool 2 has four species of sea urchins with the following numbers: A = 14, B = 2, C = 2, D = 2.

a. Compute the Shannon diversity index of the sea urchin communities in the two pools.

b. Which pool has the greater species richness? Which community is the more diverse according to the Shannon diversity index?

Estimating the number and relative abundance of species requires various sampling techniques and may be difficult due to the rarity of most species in a community. The diversity and richness of bacterial communities may be determined using molecular tools such as RFLP analysis.

Diversity and Community Stability Long-term experiments on plant diversity have shown that increased diversity correlates with increased productivity and stability of a community. The tunicate experiment in Long Island Sound indicated that more diverse communities use more of the available resources, making it more difficult for an **invasive species** to become established outside its native range.

Trophic Structure The feeding relationships in a community determine its **trophic structure**. A **food chain** shows the transfer of food energy from one trophic level to the next: from producers to herbivores (primary consumers) to carnivores (secondary, tertiary, or quaternary consumers) and eventually to decomposers.

A food web diagrams the complex trophic relationships within a community. The complicated connections of a food web arise because many consumers feed at various trophic levels. Food webs can be simplified by grouping species into functional groups (such as primary consumers) or by isolating partial food webs.

Within a food web, each food chain usually consists of five or fewer links. According to the **energetic hypothesis**, food chains are limited by the inefficiency of energy transfer from one trophic level to the next. Only about 10% of the **biomass** (total mass of all individuals) of one trophic level is converted to the biomass of the next. The **dynamic stability hypothesis** suggests that short food chains are more stable. Any environmental disruption will be magnified at higher trophic levels as food supply is reduced all the way up the chain. The increasing size of animals at successive trophic levels may also limit food chain length.

INTERACTIVE QUESTION 54.5

Experimental data from tree hole communities showed that food chains were longest when food supply (leaf litter) was greatest. Which hypothesis about food chain length do these results support?

Species with a Large Impact A **dominant species** in a community has the greatest abundance or largest biomass and is a major influence on the presence and distribution of other species. A species may become dominant due to its more competitive use of resources or its success at avoiding predation or disease. Invasive species may reach high biomass levels due to the lack of natural predators and pathogens. The removal of a dominant species from a community may adversely affect any species that relied exclusively on that species, but its role may quickly be filled by other species.

A **keystone species** has a large impact on community structure as a result of its ecological role. Paine's study of a predatory sea star demonstrated its role in maintaining species richness in an intertidal community by reducing the density of mussels, a highly competitive prey species.

Ecosystem engineers or "foundation species" influence community structure by changing the physical environment.

Bottom-Up and Top-Down Controls Arrows can be used to indicate the effect an increase in the biomass in one trophic level has on another trophic level. $V \rightarrow H$ indicates that an increase in vegetation (V) increases the number of herbivores (H); $V \leftarrow H$ indicates that an increase in herbivores decreases vegetation biomass. $V \leftrightarrow H$ means that each trophic level is affected by changes in the other. According to the **bottom-up model** of community organization, $N \rightarrow V \rightarrow H \rightarrow P$; that is, an increase in mineral nutrients (N) yields an increase in biomass at each succeeding trophic level: vegetation, herbivores, and predators (P). The **top-down model**, $N \leftarrow V \leftarrow H \leftarrow P$, assumes that predation controls community organization, with a series of +/− effects cascading down the trophic levels. According to this *trophic cascade model*, an increase in predator abundance decreases herbivore abundance, which results in increased vegetation and lowered nutrient levels.

INTERACTIVE QUESTION 54.6

Many freshwater communities appear to be organized along the top-down model. What actions might ecologists take if they wanted to use **biomanipulation** to control excessive algal blooms in a lake with four trophic levels (algae, zooplankton, primary predator fish, and top predator fish)?

54.3 Disturbance influences species diversity and composition

Traditionally, biological communities were viewed as existing in a state of equilibrium maintained by interspecific interactions. The ability of a community to reach and maintain this relatively constant species composition is known as stability. The **nonequilibrium model**, in contrast, emphasizes that communities are constantly changing as a result of **disturbances**. Disturbances such as fire, drought, storms, overgrazing, or human activities may change resource availability and reduce or eliminate some populations.

Characterizing Disturbance According to the **intermediate disturbance hypothesis**, moderate intensity or frequency of disturbance may result in greater species diversity than either low or high levels of disturbance. Small-scale disturbances may enhance environmental patchiness, helping to maintain species diversity. Human prevention of some natural disturbances, such as small fires, may lead to large-scale disturbances, such as large, destructive fires to which species may not be adapted.

Ecological Succession The sequential transitions in species composition in a community, usually following a severe disturbance, are known as ecological succession. If no soil was originally present, as on a new volcanic island or on the moraine left by a retreating glacier, the process is called **primary succession** and may take hundreds or thousands of years. A series of colonizers usually begins with autotrophic and heterotrophic prokaryotes and protists and then moves through lichens, mosses, grasses, shrubs, and trees until the community reaches its prevalent form of vegetation.

Secondary succession occurs when a community is disrupted by fire, logging, or farming, but the soil remains intact. Herbaceous species may colonize first, followed by woody shrubs and eventually trees.

Early colonizers may either *facilitate* the arrival of other species by improving the environment or *inhibit* the establishment of later species. Or species may be independent in their colonization and *tolerate* the conditions created by early species.

Ecologists have studied moraine succession during the retreat of glaciers at Glacier Bay in Alaska. The first pioneering plant species include mosses and fireweed. *Dryas*, a mat-forming shrub, dominates after about 30 years. Alder thickets are the dominant vegetation a few decades later, followed by Sitka spruce. The community becomes a spruce-hemlock forest by the third century after glacial retreat, except in flat, poorly drained areas, where sphagnum mosses invade. These mosses make the soil waterlogged and acidic, killing the trees and creating sphagnum bogs.

INTERACTIVE QUESTION 54.7

a. Describe the effects of the alder stage on soil fertility during the succession following the retreat of a glacier.

b. What is the effect of the spruce forest on soil pH?

Human Disturbance Human activities, such as converting land to agriculture, logging, clearing for urban development, and ocean trawling, have altered the structure of communities all over the world. A common result is a reduction in species diversity.

54.4 Biogeographic factors affect community diversity

Latitudinal Gradients Surveys of plant and animal species have documented much greater numbers of species in tropical habitats than in temperate and polar regions. Tropical communities are older, partly because of their longer growing season and partly because they have not had to "start over" after glaciation, as has been the case several times for many polar and temperate communities.

Solar energy input and water availability are important climatic explanations for the latitudinal gradient in diversity. **Evapotranspiration,** the amount of water evaporated from soil and transpired by plants, is determined by solar energy, temperature, and water availability. *Potential evapotranspiration* is determined by just solar radiation and temperature. Evapotranspiration rates have been shown to correlate with species richness for trees and vertebrates in North America.

INTERACTIVE QUESTION 54.8

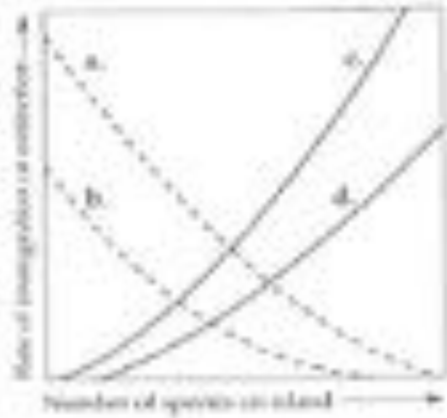
Why would the fact that tropical communities are "older" than temperate or polar communities contribute to greater species diversity?

Area Effects A **species-area curve** represents the correlation between the geographic size of a community and the number of species in it. In general, the larger the area, the greater is the diversity of habitats, and the greater the species richness. Use of such curves in conservation biology can enable scientists to predict how a loss of habitat may affect diversity.

Island Equilibrium Model Any habitat surrounded by a significantly different habitat is considered an island and allows ecologists to study factors that affect species diversity. In the 1960s, R. MacArthur and E. O. Wilson developed an island equilibrium model, which states that the size of the island and its closeness to the mainland (or source of dispersing species) are important variables directly correlated with species diversity. The rates of immigration and extinction change as the number of species on the island increases. When the rates become equal, species diversity reaches an equilibrium, although species composition may continue to change.

INTERACTIVE QUESTION 54.9

Many biogeographic studies have found that large islands have greater species richness than small islands. Label the lines for the immigration and extinction rates for a large and small island on the following graph, which shows how these rates vary with the number of species on the island. Indicate the location of the equilibrium number on the *x*-axis for a small island and for a large island.



54.5 Pathogens alter community structure locally and globally

Pathogens are disease-causing microorganisms, viruses, viroids, or prions. They can be particularly virulent when introduced into a new habitat, where host species have not yet evolved resistance or where natural controls are lacking.

Pathogens and Community Structure Pathogens have altered terrestrial ecosystems when dominant tree species are killed and are changing the community structure in coral reef communities. Global travel and trade contribute to the spread of pathogens.

Community Ecology and Zoonotic Diseases Many human diseases are caused by **zoonotic pathogens,** which are disease-causing agents transferred to humans from other animals, often by means of a **vector** such as ticks or mosquitoes. Understanding species interactions and identifying both hosts and vectors help to combat and control the spread of such diseases. Researchers used genetic and ecological data to identify two inconspicuous shrew species as the primary host of the Lyme pathogen. Infected ticks then transmit Lyme disease to people.

INTERACTIVE QUESTION 54.10

Why are ecologists trapping and testing migrating birds in Alaska?

Word Roots

crypto- = hidden, concealed (*cryptic coloration*: camouflage that makes a potential prey difficult to spot against its background)

ecto- = outer (*ectoparasite*: a parasite that feeds on the external surface of a host)

endo- = inner (*endoparasite*: a parasite that lives within a host)

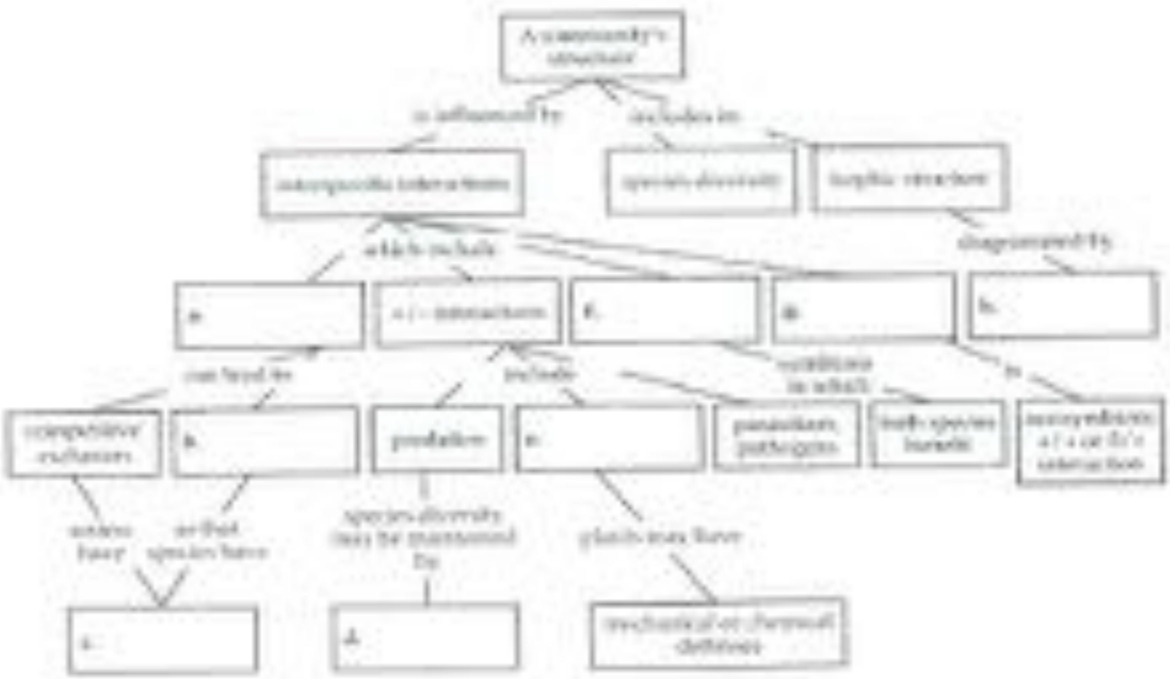
herbi- = grass; **-vora** = eat (*herbivory*: an interaction in which an organism eats parts of a plant or alga)

inter- = between (*interspecific competition*: competition for resources between individuals of two or more species when resources are in short supply)

mutu- = reciprocal (*mutualism*: a symbiotic relationship in which both participants benefit)

Structure Your Knowledge

1. Complete the following concept map to organize your understanding of the important factors that structure a community.



2. Community ecologists develop models or hypotheses to describe community structure and the factors that contribute to such structure. Briefly explain the following models described in this chapter.
   a. Competitive exclusion principle
   b. Energetic hypothesis
   c. Dynamic stability hypothesis
   d. Bottom-up model
   e. Top-down (trophic cascade) model
   f. Nonequilibrium model
   g. Island equilibrium model

Test Your Knowledge

MULTIPLE CHOICE: *Choose the one best answer.*

1. Two allopatric species of Galápagos finches have beaks of similar size. The observation that significant differences in beak size occur when the two species occur on the same island is an example of
   a. competitive exclusion.
   b. species diversity.
   c. commensalism.
   d. character displacement.
   e. a trophic cascade.

2. Aposematic coloring is most commonly found in
   a. prey whose body morphology is cryptic.
   b. predators that are able to sequester toxic plant compounds in their bodies.
   c. prey species that have chemical defenses.
   d. palatable prey that resemble each other.
   e. plants that have toxic secondary compounds.

3. Two species, A and B, occupy adjoining environmental patches that differ in several abiotic factors. When species A is experimentally removed from a portion of its patch, species B colonizes the vacated area and thrives. When species B is experimentally removed from a portion of its patch, species A does not successfully colonize the area. From these results you might conclude that
   a. both species A and species B are limited to their range by abiotic factors.
   b. species A is limited to its range by competition, and species B is limited by abiotic factors.
   c. both species are limited to their range by competition.
   d. species A is limited to its range by abiotic factors, and species B is limited to its range because it cannot compete with species A.
   e. species A is a predator of species B.

4. Through resource partitioning,
   a. two species can compete for the same prey item.
   b. slight variations in niche allow closely related species to coexist in the same habitat.
   c. two species can share identical niches in a habitat.
   d. competitive exclusion results in the success of the superior species.
   e. two species with identical niches do not share the same habitat and thus avoid competition.

5. A palatable (good-tasting) prey species may defend against predation by
   a. Müllerian mimicry.
   b. Batesian mimicry.
   c. producing secondary compounds.
   d. cryptic coloration.
   e. either b or d.

6. The species richness of a community refers to
   a. the relative numbers of individuals in each species.
   b. the number of different species found in the community.
   c. the feeding relationships or trophic structure within the community.
   d. the species diversity of that community.
   e. the community's stability or ability to persist through disturbances.

7. Which of the following organisms is mismatched with its trophic level?
   a. algae—producer
   b. phytoplankton—primary consumer
   c. carnivorous fish larvae—secondary consumer
   d. eagle—tertiary or quaternary consumer
   e. Both b and c are mismatched.

8. Ecologists survey the tree species in two forest plots. Plot 1 has six different species, and 95% of all trees belong to just one species. Plot 2 has five different species, each of which is represented by approximately 20% of the trees. Compared with plot 1, plot 2 has
   a. higher species richness.
   b. greater species diversity.
   c. lower relative abundance.
   d. lower species richness.
   e. Both b and d are correct.

9. When one species was removed from a tide pool, the pool's species diversity was significantly reduced. The removed species was probably
   a. a strong competitor.
   b. a potent parasite.
   c. a resource partitioner.
   d. a keystone species.
   e. the species with the highest relative abundance.

10. Invasive species often reach a large biomass because
   a. they are better competitors than native species.
   b. they are usually producers and not top predators.
   c. they often lack natural predators or pathogens.
   d. their superior ability to disperse enables them to spread to new niches.
   e. they are often protected by the humans who have introduced them.

11. Why do most food chains consist of only three to five links?
   a. There are only five trophic levels: producers, primary, secondary, and tertiary consumers, and decomposers.
   b. Most communities are controlled bottom-up by mineral nutrient supply.
   c. The dominant species in most communities consumes the majority of prey; thus, not enough food is left to support higher predators.
   d. According to the energetic hypothesis, the inefficiency of energy transfer from one trophic level to the next limits the number of links.
   e. According to the trophic cascade model, increasing the biomass of top trophic levels causes a decrease in the biomass of lower levels, so that the top levels are limited.

12. According to the top-down (trophic cascade) model of community control, which trophic level would you decrease if you wanted to increase the vegetation level in a community?
   a. nutrients
   b. vegetation
   c. secondary consumers (carnivores)
   d. tertiary consumers
   e. carnivores

13. During succession, inhibition by early species
   a. may prevent the achievement of a stable community.
   b. may slow down both the rate of immigration and the rate of extinction, depending on the size of the area and the distance from the source of dispersing species.
   c. results from the frequent disturbances that often eliminate early colonizers.
   d. may slow down the successful colonization by other species.
   e. may involve changes in soil pH or accelerated accumulation of humus.

14. According to the nonequilibrium model,
   a. chance events such as disturbances play major roles in the structure and composition of communities.
   b. species composition in a community is always in flux as a result of human interventions.
   c. food chains are limited to a few links because long chains are more unstable in the face of environmental disturbances.
   d. the communities with the most diversity have the least stability or resistance to change.
   e. early colonizers inhibit other species, whereas later colonizers facilitate the arrival of new species.

15. Which of the following organisms is *mismatched* with its community role?
   a. beaver—ecosystem engineer
   b. a black rush *Juncus* in a salt marsh—facilitator
   c. a sea otter in the North Pacific—keystone predator
   d. trees in a spruce-hemlock forest—dominant species
   e. alder and *Dryas* (a mat-forming shrub)—inhibitors

16. An island that is small and far from the mainland, in contrast to a large island close to the mainland, would be expected to
   a. have lower species diversity.
   b. be in an earlier successional stage.
   c. have higher species diversity but a much lower abundance of organisms.
   d. have a higher rate of colonization but a higher rate of extinction.
   e. have a lower rate of colonization and a lower rate of extinction.

17. A major explanation for the decline in species richness along an equatorial-polar gradient is the correlation of high levels of solar radiation and water availability with diversity. Which of the following factors is also thought to contribute to the high species richness of tropical communities?
   a. the inverse relationship between diversity and evapotranspiration
   b. the greater age of these communities (longer growing season and fewer climatic setbacks), providing more time for speciation events
   c. the larger area of the tropics and corresponding richness predicted by the species-area curve
   d. the lack of disturbances in tropical areas
   e. the greater immigration rate and lower extinction rate found on large tropical islands

18. Which of the following descriptions best describes a zoonotic pathogen?
   a. a pathogen that affects insects
   b. a pathogen that requires a vector to spread from animal to animal
   c. a disease-causing agent that is transmitted to humans from other animals
   d. a pathogen that is found in zoos due to the unnatural habitat provided for animals
   e. an ectoparasite that is transferred from animals to humans

Chapter 55

Ecosystems and Restoration Ecology

Key Concepts

55.1 **Physical laws govern energy flow and chemical cycling in ecosystems**

55.2 **Energy and other limiting factors control primary production in ecosystems**

55.3 **Energy transfer between trophic levels is typically only 10% efficient**

55.4 **Biological and geochemical processes cycle nutrients and water in ecosystems**

55.5 **Restoration ecologists help return degraded ecosystems to a more natural state**

Framework

This chapter describes energy flow and chemical cycling through ecosystems. Producers convert solar energy into chemical energy, which passes, with a loss of energy at each trophic level, through the ecosystem and dissipates as heat. Chemical elements are cycled within the ecosystem from inorganic reservoirs through producers, consumers, and detritivores, and back to the reservoirs.

An ecosystem's primary production may be limited by nutrients, temperature, or moisture. The low trophic efficiency in the transfer of energy from one level to the next is reflected in pyramids of production and biomass.

Bioremediation and biological augmentation are both used by restoration ecologists to help restore polluted or damaged ecosystems.

Chapter Review

An **ecosystem** consists of all the organisms in a given area and the abiotic factors with which they interact. Most ecosystems are powered by energy from sunlight, which is transformed to chemical energy by autotrophs, passed to heterotrophs in the organic compounds of food, and continually dissipated in the form of heat. Chemical elements are cycled among the abiotic and biotic components of the ecosystem as autotrophs incorporate them into organic compounds and the processes of metabolism and decomposition return them to the soil, air, and water.

55.1 Physical laws govern energy flow and chemical cycling in ecosystems

Conservation of Energy According to the first law of thermodynamics, energy can neither be created nor destroyed, only transferred or transformed. Energy flows through ecosystems from its input as solar radiation to its conversion into chemical energy to its dissipation as heat. The second law of thermodynamics states that every energy exchange increases entropy. Thus, in each energy conversion, some energy is lost as heat.

Conservation of Mass The **law of conservation of mass** states that matter cannot be created or destroyed. Ecosystem ecologists measure the inputs and outputs of elements as well as chemical cycling within ecosystems.

INTERACTIVE QUESTION 55.1

What may happen if the input of an element into an ecosystem is less than the output of that element from the ecosystem?

Energy, Mass, and Trophic Levels Most **primary producers**, or autotrophs, use light energy to synthesize organic compounds for use as fuel and building materials. Heterotrophs depend on autotrophs for their organic compounds. Primary consumers are herbivores, secondary consumers are carnivores. Tertiary consumers eat other carnivores.

Detritivores, or decomposers, consume detritus, which includes organic wastes, fallen leaves, and dead organisms. Detritivores often form a link between producers and consumers. Fungi and prokaryotes are important detritivores in most ecosystems, converting organic materials from all trophic levels to inorganic compounds that can be recycled by autotrophs.

INTERACTIVE QUESTION 55.2

Compare the movement of energy and chemical elements in ecosystems.

55.2 Energy and other limiting factors control primary production in ecosystems

Primary production is the amount of light energy converted to chemical energy during a period of time—that is, the photosynthetic output of an ecosystem's autotrophs.

Ecosystem Energy Budgets Only a small portion of incoming solar radiation strikes photosynthetic organisms, and, of that, only about 1% is converted to chemical energy. Nevertheless, worldwide photosynthetic production is about 150 billion metric tons of organic material per year.

Net primary production (NPP), which represents the chemical energy available to consumers in an ecosystem, is equal to an ecosystem's **gross primary production (GPP)** minus the energy used by autotrophs in their cellular respiration (R_a).

$$NPP = GPP - R_a$$

Net primary production can be expressed as energy ($J/m^2 \cdot yr$) or as new biomass produced, expressed as dry weight of vegetation ($g/m^2 \cdot yr$). Standing crop is the total biomass of photosynthetic organisms in an ecosystem.

Because photosynthesizing vegetation absorbs more wavelengths of visible light, scientists can estimate primary production using data from satellites that compare the wavelengths of light reflected from Earth's surface. Primary production and the contribution to Earth's total production vary by ecosystem.

Net ecosystem production (NEP), which reflects total biomass accumulation in an ecosystem, deducts the energy used in respiration by all autotrophs and heterotrophs (R_T) from gross primary production:

$$NEP = GPP - R_T$$

Scientists estimate NEP by measuring the net flux of CO_2 from terrestrial ecosystems, or the net flux of CO_2 or O_2 in oceans. Researchers using oxygen sensors on profiling floats that rise through the water column have shown greater phytoplankton productivity in nutrient-poor regions of the oceans than previously thought.

Primary Production in Aquatic Ecosystems The depth to which light penetrates and the availability of nutrients affect primary production in oceans and lakes. Nitrogen or phosphorus is often the **limiting nutrient** in the photic zone of the ocean. Nutrient enrichment experiments can identify, for example, whether nitrogen or phosphate pollution is causing algal "blooms," or which nutrient limits phytoplankton growth in the Sargasso Sea.

In freshwater lakes, nutrient limitation also affects production. **Eutrophication**, the rapid growth of cyanobacteria and algae, has been linked to phosphorus pollution from sewage and fertilizer runoff.

Primary Production in Terrestrial Ecosystems There is usually a positive correlation between primary production and precipitation. Another predictor of primary production—actual evapotranspiration, the annual amount of water evaporated from a landscape and transpired by plants—reflects both precipitation and temperature.

Nutrients affect primary production, and nitrogen and/or phosphorus are the limiting nutrients in many terrestrial ecosystems. Plant adaptations that increase uptake of nutrients include symbiotic relationships between roots and nitrogen-fixing prokaryotes, and mycorrhizal associations with fungi that provide phosphorus and other elements to plants. Plant root hairs increase absorptive surface area, and roots release substances that increase the availability of nutrients.

INTERACTIVE QUESTION 55.3

a. List some ecosystems with high primary production.

b. List some ecosystems with low primary production.

c. The oceans have low primary production yet contribute as much global net primary production as terrestrial areas. Explain.

d. Areas of the Antarctic Ocean are often more productive than tropical seas, even though they are colder and receive lower light intensity. Explain.

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

The production of new biomass from the energy contained in consumers' food during a given time is called **secondary production**.

Production Efficiency Herbivores consume only a fraction of the plant material produced; they cannot digest all they eat; and much of the energy they do absorb is used for cellular respiration. Only the chemical energy stored as growth or in offspring is available as food to secondary consumers. The proportion of assimilated food energy (not including losses in feces) that is used for net secondary production (growth and reproduction) is a measure of the efficiency of energy transformation: **production efficiency** = (net secondary production × 100%)/assimilation of primary production. Production efficiencies vary from 1–3% for endothermic birds and mammals, to 10% for fishes, to around 40% for insects and microorganisms.

Trophic Efficiency and Ecological Pyramids **Trophic efficiency** is the percentage of the production of one trophic level that makes it to the next level; it typically ranges from 5% to 20%. A *pyramid of net production* shows this multiplicative loss of energy.

A *biomass pyramid* illustrates the standing crop biomass of organisms at each trophic level. This pyramid usually narrows rapidly from producers to the top trophic level. Some aquatic ecosystems have inverted biomass pyramids in which zooplankton (consumers) outlive and outweigh the highly productive, but heavily consumed, phytoplankton. Phytoplankton have a short turnover time, the time required to replace a population's standing crop; turnover time is determined by dividing standing crop biomass by production. The production pyramid for such an aquatic ecosystem, however, is normal in shape.

INTERACTIVE QUESTION 55.4

a. Why is production efficiency higher for fishes than for birds and mammals?

b. Assuming a 10% trophic efficiency (transfer of energy to the next trophic level), approximately what proportion of the chemical energy produced in photosynthesis makes it to a tertiary consumer?

55.4 Biological and geochemical processes cycle nutrients and water in ecosystems

Chemical elements are passed between abiotic and biotic components of ecosystems through **biogeochemical cycles**.

Biogeochemical Cycles Gaseous forms of carbon, oxygen, sulfur, and nitrogen have global cycles. Heavier elements, such as phosphorus, potassium, and calcium, have a more local cycle, especially in terrestrial ecosystems.

Nutrients are found in four types of reservoirs: organic material in living organisms or detritus, which is available to other organisms; unavailable organic material in "fossilized" deposits; available inorganic elements and compounds in water, soil, or air; and unavailable elements in rocks. Nutrients may leave the unavailable reservoirs through the weathering of rock, erosion, or the burning of fossil fuels.

Ecologists study the movement of elements by tracking added radioactive isotopes or by following naturally occurring nonradioactive isotopes through ecosystems.

Exploring Nutrient Cycles The water cycle involves solar energy-driven evaporation from oceans and evapotranspiration from land, condensation of water vapor into clouds, and precipitation. Runoff and groundwater flow return water to the oceans.

In the carbon cycle, producers use CO_2 from the atmosphere in photosynthesis, producing organic compounds that are used by producers and consumers. Organisms release CO_2 in cellular respiration. Fossil fuel combustion is increasing atmospheric CO_2. Reservoirs of carbon include fossil fuels, dissolved carbon compounds in oceans, plant and animal biomass, CO_2 in the atmosphere, and sedimentary rocks such as limestone.

Plants require nitrogen in the form of ammonium (NH_4^+) or nitrate (NO_3^-). Animals obtain nitrogen in organic form from plants or other animals. The major reservoir is the atmosphere, and nitrogen enters ecosystems through *nitrogen fixation* when soil bacteria convert N_2 into compounds that can be assimilated by plants. Fertilizers and the planting of legume crops now add more nitrogen to ecosystems than do natural processes. Large quantities of reactive nitrogen gases are released to the atmosphere by human activities.

Weathering of rock adds phosphorus to the soil in the form of PO_4^{3-}, which is absorbed by plants. Organic phosphate is transferred from plants to consumers and returned to the soil through the action of decomposers or in animal excretion. Soil particles bind phosphate, keeping it available locally for recycling. Sedimentary rocks of marine origin are the largest reservoirs.

INTERACTIVE QUESTION 55.5

What is the biological importance of water, carbon, nitrogen, and phosphorus?

Decomposition and Nutrient Cycling Rates Temperature and the availability of water influence decomposition rates; thus, nutrient cycling times vary in different ecosystems. Nutrients cycle rapidly in a tropical rain forest; the soil contains only about 10% of the ecosystem's nutrients. Decomposition is slower in temperate forests, and 50% of the ecosystem's organic material may be found in detritus and soil. Decomposition rates are slow where oxygen is limited, such as in peat lands and aquatic sediments.

Case Study: Nutrient Cycling in the Hubbard Brook Experimental Forest A team of scientists has looked at nutrient cycling in the Hubbard Brook forest ecosystem since 1963. The mineral budget for each of six valleys was determined by measuring the input of key nutrients in rainfall and their outflow through the creek that drained each watershed. Most minerals were recycled within the forest ecosystem.

The effect of deforestation on nutrient cycling was measured for three years in a valley that was completely logged. Compared with a control area, water runoff from the deforested valley increased 30–40%; net loss of minerals such as Ca^{2+} and K^+ was large. Nitrate increased in concentration in the creek 60-fold, removing this critical soil nutrient and contaminating the water.

INTERACTIVE QUESTION 55.6

a. In which natural ecosystem do nutrients cycle the fastest? Why?

b. In which natural ecosystems do nutrients cycle slowly? Why?

c. What is the effect of loss of vegetation on nutrient cycling?

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

Areas degraded by farming, mining, or environmental pollution are often abandoned. In order to speed the successional processes involved in a community's recovery, restoration ecologists attempt to identify and manipulate the factors that most limit recovery time. In some cases, the physical structure of a site must first be reconstructed.

Bioremediation **Bioremediation** uses prokaryotes, fungi, or plants to detoxify polluted ecosystems. Some plants are able to extract metals from contaminated soils; harvesting those plants removes the metals from the ecosystem. Prokaryotes can metabolize dangerous elements to less soluble forms.

Biological Augmentation **Biological augmentation** uses organisms to add essential substances to degraded ecosystems. Restoration ecologists may also reintroduce animals to restored sites.

Restoration Projects Worldwide Restoration ecologists often apply adaptive management, in which they experiment with promising management approaches and learn as they work in each unique and complex disturbed ecosystem.

INTERACTIVE QUESTION 55.7

Give an example of bioremediation and of biological augmentation.

Word Roots

bio- = life; **geo-** = Earth (*biogeochemical cycle*: the various chemical cycles involving both biotic and abiotic components of ecosystems)

detrit- = wear off; **-vora** = eat (*detritivore*: a consumer that derives its energy and nutrients from nonliving organic material)

Structure Your Knowledge

1. Two processes that emerge at the ecosystem level of organization are energy flow and chemical cycling. Develop a concept map that describes, compares and contrasts these two processes.
2. What factors limit primary production in aquatic ecosystems? In terrestrial ecosystems?
3. What processes mediate the interconversion of the nutrients contained in organic materials and inorganic materials?

Test Your Knowledge

MULTIPLE CHOICE: *Choose the one best answer.*

1. Which of the following components are absolutely essential to the functioning of any ecosystem?
   a. producers and primary consumers
   b. producers and secondary consumers
   c. primary, secondary, and tertiary consumers
   d. primary consumers and detritivores
   e. producers and detritivores
2. Which of the following statements about ecosystems is true?
   a. Energy is recycled through the trophic structure.
   b. Energy is usually converted from sunlight by primary producers, passed to secondary producers in the form of organic compounds, and lost to decomposers in the form of heat.
   c. Chemicals are recycled between the biotic and abiotic sectors, whereas energy makes a one-way trip through the food web and is eventually dissipated as heat.
   d. There is a continuous process by which energy is lost as heat, and chemical elements leave the ecosystem through runoff.
   e. A food web shows that all trophic levels may feed off each other.
3. Primary production
   a. is equal to the standing crop of an ecosystem.
   b. is limited by light, nutrients, and moisture in all ecosystems.
   c. is the amount of light energy converted to chemical energy per unit time in an ecosystem.
   d. is inverted in some aquatic ecosystems.
   e. is all of the above.
4. In the experiment in which iron was added to areas of the Pacific Ocean, the growth of eukaryotic phytoplankton was stimulated because
   a. iron was the limiting nutrient for eukaryotic phytoplankton growth.
   b. the iron interacted with bottom sediments, releasing nitrogen into the water.
   c. the iron interacted with phosphorus, making that nutrient available to the phytoplankton.
   d. the iron reached the critical level necessary to promote photosynthesis.
   e. the iron stimulated the growth of nitrogen-fixing cyanobacteria, which then made nitrogen available for phytoplankton growth.
5. The open ocean and tropical rain forest are the two largest contributors to Earth's net primary production because
   a. both have high rates of net primary production.
   b. both cover huge surface areas of Earth.
   c. nutrients cycle rapidly in these two ecosystems.
   d. the ocean covers a huge surface area and the tropical rain forest has a high rate of production.
   e. both a and b are correct.
6. Production in terrestrial ecosystems is affected by
   a. temperature.
   b. light intensity.
   c. availability of nutrients.
   d. availability of water.
   e. all of the above.

7. Which of the following statements concerning net ecosystem production and net primary production is *false*?
   a. NEP will always be less than NPP because it takes the respiration of heterotrophs and decomposers into account.
   b. NEP is a means of measuring the total biomass accumulation in an ecosystem over a period of time.
   c. If measurements indicate that more CO_2 enters an ecosystem than leaves, NEP would be positive.
   d. If measurements indicate that more O_2 leaves an ecosystem than enters, NEP would be negative.
   e. An increase in the rate of decomposition in an ecosystem would lower NEP, but NPP would probably remain the same or perhaps increase.

8. Secondary production
   a. is measured by the standing crop.
   b. is the rate of biomass production in consumers.
   c. is greater than primary production.
   d. is 10% less than primary production.
   e. is the gross primary production minus the energy used for respiration.

9. Which of the following statements concerning a pyramid of net production is not true?
   a. Only about 10% of the energy in one trophic level passes into the next level.
   b. Because of the loss of energy at each trophic level, most food chains are limited to three to five links.
   c. The pyramid of production of some aquatic ecosystems is inverted because of the large zooplankton primary consumer level.
   d. Eating grain-fed beef is an inefficient means of obtaining the energy trapped by photosynthesis.
   e. A biomass pyramid is usually the same shape as a pyramid of production.

10. In which of the following groups of organisms would you expect production efficiency to be the greatest?
    a. amphibians
    b. mammals
    c. insects and microorganisms
    d. fishes
    e. birds

11. Biogeochemical cycles are global for elements
    a. that are found in the atmosphere.
    b. that are found mainly in the soil.
    c. such as carbon, nitrogen, and phosphorus.
    d. that are dissolved in water.
    e. both a and c are correct.

12. Which of these processes is incorrectly paired with its description?
    a. nitrification—oxidation of ammonium in the soil to nitrite and nitrate
    b. nitrogen fixation—reduction of atmospheric nitrogen to ammonia
    c. denitrification—return of N_2 to air; occurs when denitrifying bacteria metabolize nitrate
    d. ammonification—decomposition of organic compounds to ammonium
    e. deforestation—increased supply of nitrate in the soil

13. Clear-cutting tropical forests yields agricultural land with limited productivity because
    a. it is too hot in the tropics for most food crops.
    b. the tropical forest regrows rapidly and chokes out agricultural crops.
    c. few of the ecosystem's nutrients are stored in the soil; most are in the forest trees.
    d. phosphorus, not nitrogen, is the limiting nutrient in these soils.
    e. decomposition rates are high but primary production is low in the tropics.

14. Which of the following was not shown by the Hubbard Brook Experimental Forest study?
    a. Most minerals recycle within a forest ecosystem.
    b. Deforestation results in a large increase in water runoff.
    c. Mineral losses from a valley were great following deforestation.
    d. Nitrate was the mineral that showed the greatest loss.
    e. Acid rain increased as a result of deforestation.

15. Which of the following actions is an example of bioaugmentation?
    a. adding fertilizer to degraded soils
    b. restoring the natural flow of river channels
    c. planting nitrogen-fixing legumes in soils disturbed by mining
    d. establishing habitat corridors to connect restored sites with undisturbed sites
    e. adding ethanol to stimulate the growth of uranium-reducing bacteria in contaminated groundwater

Chapter 56

Conservation Biology and Global Change

Key Concepts

56.1 **Human activities threaten Earth's biodiversity**

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

56.3 **Landscape and regional conservation help sustain biodiversity**

56.4 **Earth is changing rapidly as a result of human actions**

56.5 **Sustainable development can improve human lives while conserving biodiversity**

Framework

Biodiversity at the genetic, species, and ecosystem levels is crucial to human welfare. This chapter explores the threats to biodiversity and several of the approaches to preserving the diversity of species on Earth. Conservation biologists focus on the population size, genetic diversity, and habitat needs of endangered species and on establishing and managing nature reserves that are often in human-dominated landscapes. Human activities are causing global change through nutrient enrichment, the release of toxins, and increasing CO_2 levels in the atmosphere. Ecological research and our biophilia may help to achieve the goal of sustainable development—the long-term perpetuation of human societies and the ecosystems that support them.

Chapter Review

Conservation biology integrates all areas of biology in the effort to sustain ecosystem processes and biodiversity.

56.1 Human activities threaten Earth's biodiversity

Three Levels of Biodiversity The current high rate of extinction threatens Earth's biological diversity. Loss of the genetic diversity within and between populations lessens a species' adaptive potential.

A second level of biodiversity is species diversity. An **endangered species**, according to the U.S. Endangered Species Act (ESA), is one that is "in danger of extinction throughout all or a significant portion of its range." A **threatened species** is defined as one that is likely to become endangered. There are many well-documented examples of recent extinctions and endangered species in most taxonomic groups.

The third level of biodiversity is ecosystem diversity. A loss of a species can negatively affect other species in the ecosystem. Human activities have altered many ecosystems.

Biodiversity and Human Welfare There are both moral and practical reasons for preserving biodiversity. A loss of biodiversity is a loss of the genetic potential held in the genomes of species, such as genes for traits that could improve crops. Biodiversity is a natural resource that can provide medicines, fibers, and food.

Humans depend on Earth's ecosystems. **Ecosystem services** include such things as purification of air and water, detoxification and decomposition of wastes, nutrient cycling, flood control, pollination of crops, and soil creation and preservation. The monetary value of ecosystem services is huge.

Threats to Biodiversity The greatest threat to biodiversity is habitat destruction, caused by agriculture, urban development, forestry, mining, pollution, and global climate change. According to the International Union for Conservation of Nature and Natural Resources (IUCN), habitat destruction is implicated in 73% of species that have been designated as extinct, endangered, vulnerable, or rare. Fragmentation of natural habitats is a common occurrence and almost always leads to species loss. Both terrestrial ecosystems and aquatic habitats have been damaged.

Introduced species, sometimes called non-native or exotic species, compete with or prey upon native species. Humans have transplanted thousands of species, intentionally and unintentionally, with huge economic costs in terms of damage and control efforts.

Overharvesting involves harvesting wild plants or animals at rates higher than the populations' abilities to reproduce. Species of large animals with low reproductive rates and species on small islands are particularly vulnerable. Overfishing, particularly using new harvesting techniques, has drastically reduced populations of many commercially important fish species. The tools of molecular genetics enable conservation biologists to determine whether tissues have come from threatened or endangered species.

Global change is a threat to biodiversity at regional to global levels through alterations in climate, atmospheric chemistry, and ecological systems. The burning of fossil fuels and wood, for example, releases oxides of sulfur and nitrogen, which form sulfuric and nitric acid in the atmosphere. These acids contribute to *acid precipitation*, defined as rain, snow, sleet, or fog with a pH less than 5.2. Drifting emissions from factories create acid precipitation, which has damaged forests and fish populations in lakes across North America and Europe. New regulations and technologies have reduced sulfur dioxide emissions, and the acidity of precipitation has gradually been reduced.

INTERACTIVE QUESTION 56.1

Give an example of how each of the following threats to biodiversity has reduced population numbers or caused extinctions.

a. habitat destruction

b. introduced species

c. overharvesting

d. global change

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

Small-Population Approach According to the small-population approach, the inbreeding and genetic drift characteristic of a small population may draw it down an **extinction vortex**, in which the loss of genetic variation leads, by positive feedback loops, to smaller and smaller numbers until the population becomes extinct. Low genetic diversity, however, does not always doom a population.

The story of the greater prairie chicken provides an example of an averted extinction vortex. As agriculture fragmented their habitat, the number of prairie chickens in Illinois declined from millions in the 19th century to 50 in 1993. A comparison with DNA from museum specimens indicated decreased genetic variation in the threatened population. After importing birds from larger populations in other states, researchers noted an increase in egg viability, and the Illinois population rebounded.

Computer models that integrate many factors are used to estimate **minimum viable population (MVP)**, the minimum population size necessary to sustain a population.

The **effective population size** (N_e) is based on a population's breeding potential and is determined by a formula that includes the number of individuals that breed and the sex ratio of the population: $N_e = (4N_f N_m)/(N_f + N_m)$. Alternative formulas take into account life history or genetic factors. Conservation efforts should be based on maintaining the minimum number of reproductively active individuals needed to prevent extinction.

INTERACTIVE QUESTION 56.2

Is the effective population size usually larger or smaller than the actual number of individuals in the population? Explain.

Population viability analysis uses MVP to predict long-term viability of a population—the probability of survival over a particular period of time. M. Shaffer performed a population viability analysis as part of a long-term study of grizzly bears in Yellowstone National Park. He estimated that the minimum viable population size for threatened grizzly bear populations was 100 bears. Current estimates of the grizzly population in the greater Yellowstone ecosystem indicate a population of about 400. The effective population size, however, is only 25% of the total population size, or 100 bears. Genetic analyses indicate that the Yellowstone grizzly population has less genetic variability than other populations in North America. Migration between isolated populations could increase both the effective size and genetic variation of the Yellowstone grizzly bear population.

INTERACTIVE QUESTION 56.3

Explain the basic premise of the small population approach. What conservation strategy is recommended for preserving small populations?

Declining-Population Approach The emphasis of the declining-population approach is to identify populations that may be declining, determine the environmental factors that caused the decline, and then recommend corrective measures.

The following logical steps are part of the declining-population approach: assess population trends and distributions to establish that a species is in decline; determine its environmental requirements; list all possible causes of the decline and the predictions that arise from each of these hypotheses; test the most likely hypothesis to see if the population rebounds if this suspected factor is altered; and apply the results to the management of the threatened species.

Several factors have driven the red-cockaded woodpecker into decline. Logging and agriculture have fragmented its mature pine forest habitats, and strict fire control has resulted in excessively thick undergrowth around the pine trees. Recognition of this species' social organization and of the factors that slow its dispersal to new territories has aided in its recovery. Management strategies now include protection of some longleaf pine forests, controlled fires, and the excavation of breeding cavities in unoccupied habitats to encourage establishment of new breeding groups.

INTERACTIVE QUESTION 56.4

Describe the declining-population approach to the conservation of endangered species.

Weighing Conflicting Demands Preserving habitat for endangered species often conflicts with the economic and recreational desires of humans. Keystone species exert more influence on community structure and ecosystem processes, and prioritizing the species to be saved on the basis of their ecological role may be crucial to the survival of whole communities.

56.3 Landscape and regional conservation help sustain biodiversity

Conservation efforts increasingly are directed at sustaining the biodiversity of whole communities and ecosystems. A goal of landscape ecology is to make biodiversity conservation a part of ecosystem management and landscape use.

Landscape Structure and Biodiversity Landscape dynamics are important to conservation efforts because species often use more than one ecosystem or live on borders between ecosystems. Landscapes include ecosystems separated by boundaries or *edges*, which have their own sets of physical conditions and communities of organisms. The increase in edge communities due to human fragmentation of habitats may serve to reduce biodiversity as edge-adapted species become predominant. The long-term Biological Dynamics of Forest Fragments Project has shown that species adapted to forest interiors decline the most when habitat fragments are small.

Movement corridors are narrow strips or clumps of habitat that connect isolated patches. Artificial corridors are sometimes constructed when habitat patches have been separated by major human disruptions.

INTERACTIVE QUESTION 56.5

What are some potential benefits of corridors? How might they be harmful?

Establishing Protected Areas Currently about 7% of Earth's land area has been set aside as reserves. Conservation biologists consider landscape dynamics in the designation and management of these protected areas. Biodiversity hot spots—small areas with very high concentrations of endemic, threatened, and endangered species—are good choices for nature reserves. Global change will complicate the use of the hot-spot approach to conservation.

Even though nature reserves provide islands of protected habitat, the nonequilibrium model of natural disturbances applies to them. Patch dynamics, edges, and corridor effects must be considered in the design and management of reserves.

New information on the requirements for minimum viable population sizes indicates that most national parks and reserves are much too small—the area needed to sustain a population is usually much larger than the legal boundary set in a reserve.

INTERACTIVE QUESTION 56.6

What factors would favor the creation of larger, extensive reserves? What factors favor smaller, unconnected reserves?

Zoned reserves have protected core areas surrounded by buffer zones in which the human social and economic climate is stable and activities are regulated to promote the long-term viability of the protected zones. Costa Rica has established eight zoned reserves, but deforestation has continued in some buffer zones. The Florida Keys National Marine Sanctuary, a zoned marine reserve established in 1990, has increased marine life and generated revenue from recreational divers.

56.4 Earth is changing rapidly as a result of human actions

Nutrient Enrichment The harvesting of crops removes nutrients that would otherwise be recycled in the soil. Once the organic and inorganic reserves of soils become depleted, crops require the addition of fertilizers. The addition of nitrogen fertilizers, increased legume cultivation, and burning of fossil fuels has more than doubled Earth's supply of fixed nitrogen.

Nitrogen in excess of the **critical load**, the amount of added nutrient that can be absorbed by plants without damaging the ecosystem, can contaminate groundwater, degrade lakes and rivers, and drain into the ocean. Elevated nitrogen levels create phytoplankton blooms. The decomposition of these phytoplankton lowers oxygen levels, creating "dead zones" in coastal waters. Eutrophication of lakes due to nutrient runoff can kill fish and harm other organisms.

Toxins in the Environment Humans release a huge variety of toxic chemicals into the environment. Organisms absorb these toxins from food and water and may retain them within their tissues. In a process known as **biological magnification,** the concentration of such compounds increases in each successive link of the food chain. Chlorinated hydrocarbons (such as DDT) and polychlorinated biphenyls (or PCBs) have been implicated in endocrine system problems in many animal species. Many toxic chemicals dumped into ecosystems are nonbiodegradable; others, such as mercury, may become more harmful as they react with other environmental factors.

Greenhouse Gases and Global Warming The concentration of CO_2 in the atmosphere has been increasing since the Industrial Revolution as a result of the combustion of fossil fuel and deforestation. If C_3 plants become able to outcompete C_4 plants with the increase in CO_2, species composition in natural and agricultural communities may be altered.

In the Forest-Atmosphere Carbon Transfer and Storage (FACTS-I) experiment, scientists have monitored the effects of elevated CO_2 levels on sample plots in a forest ecosystem over many years. Trees in experimental plots have produced 15% more wood each year, although this increase is less than expected. Because of nutrient limitation, increased CO_2 levels will increase plant production somewhat less than had been predicted.

Through a phenomenon known as the **greenhouse effect,** CO_2, other greenhouse gases, and water vapor in the atmosphere absorb infrared radiation reflected from Earth and re-reflect it back, thus warming Earth.

Scientists use various models in estimating the extent and consequences of increasing CO_2 levels. A number of studies predict a doubling of CO_2 levels and a temperature rise of 3°C by the end of the twenty-first century. To predict the impact of increasing temperatures, ecologists study the effects on vegetation of previous global warming trends. Because plants cannot disperse rapidly, many may not be able to survive global climate change. One solution, although potentially dangerous, may be **assisted migration,** in which a species is moved to a habitat beyond its native range to protect it from human-caused threats.

Controlling the levels of CO_2 emissions in increasingly industrialized societies is a huge international challenge.

INTERACTIVE QUESTION 56.7

List some of the ways by which we may slow global warming.

Depletion of Atmospheric Ozone A layer of ozone molecules (O_3) in the stratosphere absorbs damaging ultraviolet radiation. This layer has been gradually thinning since the mid-1970s, largely as a result of the accumulation of breakdown products of chlorofluorocarbons in the atmosphere. The dangers of ozone depletion may include increased incidence of skin cancer and cataracts and unpredictable effects on phytoplankton, crops, and natural ecosystems.

56.5 Sustainable development can improve human lives while conserving biodiversity

Sustainable Biosphere Initiative **Sustainable development** is economic development that meets the needs of people today without limiting the ability of future generations to meet their needs. The Ecological Society of America endorses a research agenda, the Sustainable Biosphere Initiative, that encourages studies of global change, biodiversity, and maintenance of the productivity of natural and artificial ecosystems. An important goal is developing the ecological knowledge necessary to make intelligent and responsible decisions concerning Earth's resources.

Case Study: Sustainable Development in Costa Rica Partnerships between the government, nongovernment organizations (NGOs), and citizens have contributed to the success of conservation in Costa Rica. Living conditions in the country have improved, as evidenced by a decrease in infant mortality, an increase in life expectancy, and a high literacy rate. A projected increase in population from 4 million to 6 million in the next 50 years, however, will present challenges to the goal of sustainable development.

The Future of the Biosphere E. O. Wilson calls our attraction to Earth's diversity of life and our affinity for natural environments biophilia. Perhaps this connection is innate and will provide the ethical resolve needed to protect species from extinction and ecosystems from destruction. By coming to know and understand nature through the study of biology, we may become more able to appreciate and preserve the processes and diversity of the biosphere.

Word Roots

bio- = life (*biodiversity hot spot*: a relatively small area with numerous endemic species and a large number of endangered and threatened species)

Structure Your Knowledge

1. List the four major threats to biodiversity.
2. How does the loss of biodiversity threaten human welfare?
3. What do edges and movement corridors have to do with habitat fragmentation?

Test Your Knowledge

MULTIPLE CHOICE: *Choose the one best answer.*

1. According to the Endangered Species Act, a threatened species is
   a. an exotic species that cannot successfully compete with native organisms.
   b. an endemic species that is found nowhere else in the world.
   c. a species that is found in disturbed habitats.
   d. a species that is in danger of extinction in all or a large part of its range.
   e. a species that is likely to become endangered.
2. Ecosystem services include all of the following except
   a. pollination of crops.
   b. production of antibiotics and drugs.
   c. purification of air and water.
   d. decomposition of wastes.
   e. reduced impact of weather extremes.
3. The most serious threat to biodiversity is
   a. competition from introduced species.
   b. environmental toxins.
   c. habitat destruction.
   d. overharvesting.
   e. disruption of community dynamics.
4. Some grassland and conifer forest reserves have effective fire prevention programs. The most likely result of such programs is
   a. an increase in species diversity because fires are prevented.
   b. a change in community composition because fires are natural disturbances that maintain the community structure.

c. the preservation of endangered species in the area.
d. no change in the species composition of the community.
e. succession to a deciduous forest.

5. According to the small-population approach, the most important remedy for preserving an endangered species is to
a. establish a large nature reserve around its habitat.
b. control the populations of its natural predators.
c. determine the reason for its decline.
d. encourage dispersal and an increase in genetic diversity.
e. set up artificial breeding programs.

6. Which of the following characteristics is typical of biodiversity hot spots?
a. a large number of endemic species
b. a high rate of habitat degradation
c. little species diversity
d. a large land or aquatic area
e. large populations of migratory birds

7. Which of the following phenomena may occur when a population falls below its minimum viable population size?
a. genetic drift
b. a further reduction in population size
c. inbreeding
d. a loss of genetic diversity
e. All of the above are characteristics of an extinction vortex that the population may enter.

8. Movement corridors are
a. strips or clumps of habitat that connect isolated habitats.
b. the routes taken by migratory animals.
c. connections within a landscape that includes several different ecosystems.
d. the areas forming the boundary or edge between two ecosystems.
e. buffer zones for human traffic that promote the long-term viability of protected areas.

9. What does it mean if a population's effective population size (N_e) is the same as its actual population size?
a. The population is not in danger of becoming extinct.
b. The population has high genetic diversity.
c. All the members of the population breed.
d. The population's minimum viable population will not sustain the population.
e. The population is being drawn into an extinction vortex.

10. The focus of the declining-population approach to conservation is to
a. predict a species' minimum viable population size.
b. transplant members from other populations to increase genetic diversity.
c. perform a population viability analysis to predict the long-term viability of a population in a particular habitat.
d. determine the cause of a species' decline and take remedial action.
e. establish zoned reserves that ensure that human landscapes surrounding reserves support the protected habitats.

11. Given their limited resources, conservation biologists working to preserve biodiversity should assign the highest priority to
a. the northern spotted owl.
b. declining keystone species in a community.
c. a commercially important species.
d. endangered and threatened vertebrate species.
e. all declining species.

12. The finding of harmful levels of DDT in grebes (fish-eating birds) following years of trying to eliminate bothersome gnat populations in a lakeshore town is an example of
a. eutrophication.
b. biological magnification.
c. nutrient enrichment.
d. an edge effect of a landscape ecosystem.
e. increasing resistance to pesticides.

13. Which of the following phenomena is a direct effect of the thinning of the ozone layer?
a. a reduction in species diversity
b. global warming
c. acid precipitation
d. an increase in harmful UV radiation reaching Earth
e. dead zones in the Antarctic Ocean

14. Sustainable development
a. uses nature reserves to save endangered species so that the rest of Earth's ecosystems can be used for human development.
b. requires the establishment of zoned reserves.
c. is economic development that meets the needs of people today without limiting the ability of people to meet their needs in the future.
d. is the research agenda of the Sustainable Biosphere Initiative to study global change, biodiversity, and Earth's ecosystems.
e. sustains the productivity of agricultural ecosystems through the use of chemical and organic fertilizers and irrigation.