Chapter 24: Evolution by Natural Selection

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Key Concepts

- Populations and species evolve, meaning that their characteristics change through time. More precisely, evolution is defined as changes in allele frequencies over time.
- Natural selection occurs when individuals with certain alleles produce the most offspring in a population. An adaptation is a genetically based trait that increases an individual's ability to produce offspring in a particular environment.
- Evolution by natural selection is not progressive, and it does not change the characteristics of the individuals that are selected—it changes only the characteristics of the population. Animals do not do things for the good of the species, and not all traits are adaptive. All adaptations are constrained by trade-offs and genetic and historical factors.

Section 24.1: The Evolution of Evolutionary Thought

- Plato claimed that every organism was an example of a perfect essence or type created by God and that these types were unchanging.
- Aristotle ordered the types of organisms into a linear scheme called the **great chain of being** in which species were organized into a sequence based on increased size and complexity, with humans at the top.
- Lamarck was the first to propose a formal theory of **evolution**—the idea that species change through time.
- Lamarck claimed that simple organisms originate at the base of the chain by spontaneous generation and then evolve by moving up the chain over time.
- The process responsible for this progression was the inheritance of **acquired characters**.
- Darwin and Wallace proposed that evolution does not follow a linear, progressive pattern.
- Instead, they proposed that the process responsible for change through time is based on variation among individuals in populations.
- Darwin claimed that variation among individuals in a population was the key to understanding the nature of species.
- Darwin and Wallace proposed that evolution occurs because traits vary among the individuals in a population, and because individuals with certain traits leave more offspring than others do.

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Section 24.2: Pattern of Evolution: Have Species Changed through Time?

- **Evidence for Change through Time**
  - Extinction
  - Transitional Forms

–Vestigial Traits

> **Evidence That Species Are Related Geographic**

–Relationships

–Homology

> **Evolution Is Change through Time** – Darwin described evolution as **descent with modification**, meaning that change over time produced modern species from ancestral species.

> **Evidence for Change through Time**

–**Fossils** are traces of organisms that lived in the past.

–Fossils that have been found and described in the scientific literature make up the **fossil record.**

–Most fossils are found in **sedimentary rocks.**

–Layers of sedimentary rock are associated with different intervals in the **geologic time scale**—a relative time scale based upon fossil content.

–Geologic time is divided into eons, eras, periods, and epochs.

–Researchers now use radioactive isotopes to assign absolute ages to the geologic time scale.

–Geologic data show that Earth is about 4.6 billion years old.

–Fossil data show the earliest signs of life in rocks about 3.4 billion years old.

> **Extinction**

–Many fossils provide evidence for **extinct** species unlike any known living organisms.

–Darwin interpreted extinction as evidence that species are dynamic and can change.

–He reasoned that if species have gone extinct, then the array of species living on Earth has changed through time.

> **Transitional Forms**

–The law of succession means that extinct fossil species are typically succeeded, in the same region, by similar species.

–Darwin interpreted this pattern as evidence that extinct forms and living forms are related, and that they represent ancestors and descendants.

–Many **transitional forms** have been discovered with traits that are intermediate between older and younger species.

–These transitional forms provide strong evidence for change through time.

> **Vestigial Traits**

–A vestigial trait is a reduced or incompletely developed structure that has no function or reduced function, but is clearly similar to functioning organs or structures in closely related species.

–Vestigial traits are evidence that the characteristics of species have changed over time.

> **Evidence That Species Are Related** – Data from the fossil record and contemporary species refute the hypothesis that species are immutable.

> **Geographic Relationships**

–Darwin collected mockingbirds from the Galápagos islands. The mockingbirds were superficially similar, but different islands had distinct species.

–Darwin proposed that the mockingbirds were similar because they had descended from the same common ancestor.

–The mockingbird species are part of a **phylogeny**, a family tree of populations or species.

–The relationship between different species can be shown on a **phylogenetic tree.**

> **Homology** is a similarity that exists in species descended from a common ancestor.

–**Genetic homology** is similarity in the DNA sequences of different species.

–**Developmental homology** is a similarity in embryonic traits.

–**Structural homology** refers to similarities in adult morphologies.

–In many cases, traits are similar in different species because the species in question were related to each other by common descent.

–If species were created independently of one another, these types of similarities would not occur.

> **Evolution Is Change through Time** – Darwin and others have provided convincing evidence to support the idea that species have descended, with modification, from a common ancestor.

Section 24.3: The Process of Evolution: How Does Natural Selection Work?

> The idea of evolution predates Darwin, but Darwin's crucial insight lay in recognizing the process of **natural selection** that could explain the pattern of descent with modification.

> The process of evolution by natural selection can be broken down into four steps:

–Individuals that make up a population vary in the traits they possess.

–Some of these trait differences are heritable.

–Each generation, many more offspring are produced than can possibly survive. Only some individuals in the population survive long enough to produce offspring. Of these, some will produce more offspring than others.

–The subset of individuals that survive best and produce the most offspring is not a random sample of the population. Individuals with certain heritable traits are more likely to survive and reproduce. Natural selection occurs when individuals with certain characteristics produce more offspring than do individuals without those characteristics.

> Some heritable traits help an individual to survive or reproduce better than other individuals.

> These are the traits that will, over time, increase in frequency in the population, causing **evolution**—a change in the genetic characteristics of a population over time.

> Evolution by natural selection occurs when heritable variation leads to differential success in survival and reproduction.

> Evolution – change in allele frequencies in a population over time.

> **Darwinian fitness** is the ability of an individual to produce offspring, relative to that ability in other individuals in the population.

> An **adaptation** is a heritable trait that increases an individual's fitness in a particular environment relative to individuals lacking that trait. Adaptations increase fitness—the ability to produce offspring.

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> Evolution by natural selection occurs when heritable variation in traits leads to differential success in survival and reproduction.

Section 24.4: Evolution in Action: Recent Research on Natural Selection

The theory of evolution by natural selection is testable, and there are numerous examples.

How Did Mycobacterium tuberculosis Become Resistant to Antibiotics?

> Mycobacterium tuberculosis causes **tuberculosis (TB)**, a disease that killed up to a third of all adults in big cities in the nineteenth century and still kills more adult humans than any other virus or bacteria.

> Sanitation, nutrition, and antibiotics greatly reduced deaths due to TB in industrialized nations between 1950 and 1990.

> In the late 1980s, rates of TB surged due to the evolution of drug–resistant strains.

> DNA from rifampin–resistant bacteria was found to have a single point mutation in the rpoB gene that encodes a component of RNA polymerase.

> Rifampin interferes with RNA polymerase and transcription, but the C–to–T mutation prevents rifampin binding.

> Under normal conditions, mutant forms of RNA polymerase do not work as well as the normal form.

> During antibiotic therapy, cells with normal RNA polymerase grow more slowly or die, but those with mutant RNA polymerase proliferate. *Web Animation: Natural selection for antibiotic resistance

> Natural selection acts on individuals, because individuals experience differential success.
> Only populations evolve, as allele frequencies change in populations, not individuals.

Why Are Beak Size, Beak Shape, and Body Size Changing in Galapagos Finches?

> Long–term research on changes in body size and beak size and shape in medium ground finches found on Isle Daphne Major of the Galápagos Islands showed beak morphology and body size are heritable.
> A major drought led to an 84% die–off of the ground finches.
> Natural selection resulting from this drought led to an increase in the finch population's average beak depth (Figure 24.13).

> Yet another change in the population's characteristics occurred as a result of seven months of rain, during which small individuals with small, pointed beaks had exceptionally high reproductive success.
> Long term changes in body size and beak shape but not beak size occurred.

Section 24.5: The Nature of Natural Selection and Adaptation

Although natural selection appears to be a simple process, research has shown that it is often misunderstood.

Selection Acts on Individuals, but Evolutionary Change Occurs in Populations

> Individuals do not change during natural selection, only populations do.
> Natural selection acts on individuals, but evolutionary change occurs in the characteristics of a population.
> Individuals do not change when they are selected, they simply produce more surviving offspring than other individuals do.
> **Acclimation** occurs when an individual changes in response to changes in the environment, but **adaptation** occurs only when a population changes in response to natural selection.

Evolution Is Not Goal–Directed or Progressive

> Evolution by natural selection is not goal–directed. Adaptations do not occur because organisms want or need them.
> Evolution is also not progressive.
> Under evolution by natural selection, there is no such thing as "higher" or "lower" organisms (Figure 24.16).
> Species are related by a common ancestry and all have evolved through time. As evolution continues, species may become simpler or more complex, depending on which traits are favored by the environment.
> Natural selection is not goal directed or progressive.
> It simply favors individuals that happen to be better adapted to the environment at the time.

Animals Do Not Do Things for the Good of the Species

- Individuals with self–sacrificing alleles die and do not produce offspring.
- Individuals with selfish, cheater alleles survive and produce offspring.
- Selfish alleles increase in frequency while self–sacrificing alleles decrease in frequency.

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- Thus, it is not possible for individuals to sacrifice themselves for the good of the species.

Not All Traits Are Adaptive

- Adaptation is not a perfect process.
- Not all traits are adaptive, and adaptations that organisms have are constrained in a variety of important ways.

Genetic Constraints

- Selection is not able to optimize all aspects of a trait due to certain genetic constraints.

Genetic correlation – is when selection on alleles for one trait causes a correlated but suboptimal change in another trait.

Lack of genetic variation can also constrain evolution, because natural selection can work only on existing variation in a population.

Fitness Trade–offs

- A **fitness trade–off** is a compromise between traits.
- Because selection acts on many traits at once, every adaptation is a compromise.

Historical Constraints

- Because all traits evolve from previously existing traits, adaptations are constrained by history.
- Not all traits are adaptive, and even adaptive traits are constrained by genetic and historical factors.

Chapter 25: Evolutionary Processes

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Key Concepts

- The Hardy-Weinberg principle acts as a null hypothesis when researchers want to test whether evolution or nonrandom mating is occurring at a particular gene.
- Each of the four evolutionary mechanisms has different consequences. Only natural selection produces adaptation. Genetic drift causes random fluctuations in allele frequencies. Gene flow equalizes allele frequencies between populations. Mutation introduces new alleles.
- Inbreeding changes genotype frequencies but does not change allele frequencies.
- Sexual selection leads to the evolution of traits that help individuals attract mates. It is usually stronger on males than on females.

Section 25.1: Analyzing Change in Allele Frequencies: The Hardy-Weinberg Principle

- G. H. Hardy and Wilhelm Weinberg developed a mathematical model to analyze the consequences of mating among all of the individuals in a population.
- Their calculations would predict the genotypes of the offspring that would be produced, as well as the frequency of each genotype.
- For a gene with two alleles A_1 and A_2, three genotypes are possible: A_1A_1, A_1A_2, and A_2A_2.
- The frequency of A_1 is represented by p and the frequency of A_2 is represented by q.
- The frequency of the A_1A_1 genotype in the new generation will be p^2.
- The frequency of the A_2A_2 genotype will be q^2.
- The frequency of A_1A_2 genotype will be 2pq.
- Because all individuals in the new generation must have one of the three genotypes, the sum of the three genotype frequencies must equal 1 (100% of the population): $p^2 + 2pq + q^2 = 1$.
- When allele frequencies are calculated for this new generation, the frequency of A_1 is still 'p' and the frequency of A_2 is still q.
- The **Hardy–Weinberg principle** makes two fundamental claims:
    - –if the frequencies of alleles A_1 and A_2 in a population are given by p and q, then the frequencies of genotypes A_1A_1, A_1A_2, and A_2A_2 will be given by p^2, 2pq, and q^2 for generation after generation

    - –when alleles are transmitted according to the rules of Mendelian inheritance, their frequencies do not change over time. For evolution to occur, some other factor or factors must come into play.

The Hardy–Weinberg Model Makes Important Assumptions

- The Hardy–Weinberg model assumes that none of the four evolutionary mechanisms can be acting on the population.
- In addition, the model assumes that mating is random with respect to the gene in question.
- The Hardy–Weinberg principle holds when the following five conditions are met with respect to the gene in question:
    - –no natural selection
    - –no genetic drift or random allele frequency changes
    - –no gene flow
    - –no mutation
    - –random mating

How Does the Hardy–Weinberg Principle Serve as a Null Hypothesis?

- The Hardy–Weinberg principle serves as a null hypothesis for determining whether evolution is acting on a particular gene in a population.

- When genotype frequencies do not conform to Hardy–Weinberg proportions, evolution or nonrandom mating is occurring in that population.

Are MN Blood Types in Humans in Hardy–Weinberg Equilibrium?

- Most human populations have two alleles for the MN blood group.
- The genotype of a person can be determined from blood samples.
- To estimate the frequency of each genotype in a population, geneticists obtain data from a large number of individuals and then divide the number of individuals with each genotype by the total number of individuals in the sample.
- Analysis to determine if the Hardy–Weinberg principle holds requires four steps:
  - –estimate genotype frequencies by observation
  - –calculate observed allele frequencies from the observed genotype frequencies

  - –use the observed allele frequencies to calculate the genotypes expected according to the Hardy–Weinberg principle
  - –compare the observed and expected values.
- The observed and expected MN genotype frequencies were almost identical.
- Since the genotypes at the MN locus are in Hardy–Weinberg proportions, evolutionary processes do not currently affect MN blood groups, and mating must be random with respect to this trait.

Are HLA Genes in Humans in Hardy–Weinberg Equilibrium?

- To test the hypothesis that heterozygotes for the HLA–A and HLA–B genes might be more fit than homozygotes, the genotypes of 125 Havasupai tribe members were used to estimate population allele frequencies.
- The expected genotype frequencies did not match the observed frequencies.
- Therefore, at least one of the Hardy–Weinberg assumptions must be violated for these alleles in this population.
- Mutation, migration, and genetic drift are negligible in this case.
- There are two possible explanations for this:
  - –mating is not random with respect to the HLA genotype
  - –heterozygous individuals have higher fitness

Section 25.2 Outline: Patterns of Natural Selection

- Natural selection occurs when individuals with certain phenotypes produce more offspring than individuals with other phenotypes do.
- The alleles associated with the favored phenotypes increase in frequency

while other alleles decrease in frequency.

- **Heterozygote advantage** is a pattern of natural selection in which heterozygous individuals have higher fitness than homozygous individuals.
- **Genetic variation** refers to the number and relative frequency of alleles that are present in a particular population. Natural selection maintains genetic variation in a population.

Directional Selection

- occurs when natural selection increases the frequency of one allele.
- This type of selection reduces population genetic diversity over time

- If directional selection continues over time, the favored alleles eventually reach a frequency of 1.0.
- Disadvantageous alleles will reach a frequency of 0.0.
- Alleles that reach a frequency of 1.0 are said to be fixed. Those alleles that are no longer found in the population are said to be lost.

Stabilizing Selection

- occurs when individuals with intermediate traits reproduce more than others, thereby maintaining intermediate phenotypes in a population.
- Stabilizing selection reduces a population's genetic variation over time but does not change its average trait value.

Disruptive Selection

- is the opposite of stabilizing selection.
- It occurs when intermediate phenotypes are selected against and extreme phenotypes are favored.
- Disruptive selection maintains genetic variation but does not change the mean value of a trait.
- Disruptive selection can cause **speciation** (the formation of new species) if individuals with one extreme of a trait start mating preferentially with individual that have the same trait.

Section 25.3: Genetic Drift

Genetic drift is any change in allele frequencies due to chance (**sampling error**).

- It causes allele frequencies to drift up and down randomly over time.
- Genetic drift is random with respect to fitness.
- Allele frequency changes are not adaptive.
- Genetic drift is most pronounced in a small population.
- Over time, genetic drift can lead to the random loss or fixation of alleles.
- When random loss or fixation occurs, genetic variation in the population declines.
- Genetic drift is more pronounced in small populations than large populations.
- Given enough time, genetic drift can be an important factor even in large

populations.

Experimental Studies of Genetic Drift

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- Research on genetic drift in fruit flies used leg–bristle morphology as a **genetic marker**, a specific allele that causes a distinctive phenotype.
- In the laboratory, genetic drift was found to decrease genetic variation within populations and increase genetic differences between populations.

Genetic Drift in Natural Populations

- Genetic drift is of great concern to conservation biologists because the small populations found on nature reserves or in zoos are especially susceptible to it.

How Do Founder Effects Cause Drift?

- A **founder event** occurs when a group emigrates to a new area and starts a new population.
- If the founding group is small, its allele frequencies probably differ from those of the source population.
- This sampling effect on the new population's allele frequencies is called a **founder effect**.
- Founder events and founder effects are especially common in the colonization of isolated habitats such as islands, mountains, caves, and ponds.

How Do Population Bottlenecks Cause Drift?

- A sudden decrease in population size, called a **population bottleneck**, can lead to a **genetic bottleneck**—a sudden reduction in the number of alleles in a population.
- Genetic bottlenecks are commonly caused by disease outbreaks and natural catastrophes, and genetic drift often occurs in the resulting small population.

Section 25.4: Gene Flow

Gene flow, the movement of alleles from one population to another, occurs whenever individuals leave one population, join another, and breed.

- Gene flow equalizes gene frequencies between the source and recipient populations.
- Gene flow can increase the average fitness of individuals in a population where genetic diversity was lost due to genetic drift.
- Gene flow can decrease the average fitness of individuals in a population that was highly adapted to a specific habitat through natural selection.

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- Gene flow is random with respect to fitness, but movement of alleles between populations always tends to reduce genetic differences between them.

Section 25.5: Mutation

> Although most evolutionary mechanisms reduce genetic diversity, **mutation** restores genetic diversity and creates new alleles.
> Because errors are inevitable, mutation is always adding new alleles into populations at all gene loci.
> Most mutations result in production of **deleterious alleles**, alleles that lower fitness.
> Occasionally, mutation produces a beneficial allele that should increase in frequency in a population due to natural selection

Mutation as an Evolutionary Mechanism

> Mutation does little to change allele frequencies on its own.
> Mutation rarely causes a change from the genotype frequencies expected under the Hardy–Weinberg principle.
> As an evolutionary mechanism, mutation is extremely slow compared with selection, genetic drift, and gene flow.

What Role Does Mutation Play in Evolutionary Change?

> Escherichia coli has been used as a model to study how mutation affects evolution. E. coli is asexual, so mutation is the only source of genetic variation.
> Although no gene flow occurred, both selection and genetic drift operate in each population.
> The relative fitness of the populations was found to increase over time in jumps.
> This pattern was proposed to result from novel mutations arising and conferring a fitness benefit.
> Mutation provides the genetic variation upon which natural selection can act to produce evolution.

Section 25.6: Nonrandom Mating

In nature, mating may not be random with respect to the gene in question.

Inbreeding

> Inbreeding (mating between relatives) increases the frequency of homozygotes and reduces the frequency of heterozygotes in each generation.
> Inbreeding does not cause evolution, because allele frequencies do not change in the population as a whole.
> Inbreeding changes genotype frequencies but not allele frequencies.
> **Inbreeding depression** is a decline in average fitness that takes place when homozygosity increases and heterozygosity decreases in a population.
> Inbreeding depression results from two processes:
–inbreeding increases the frequency of homozygous recessive individuals

–many genes are under intense selection for heterozygote advantage

> Offspring of inbred matings are expected to have lower fitness than the progeny of outcrossed matings (Figure 25.11 and Table 25.5).

> Inbreeding does not cause evolution directly but can speed the rate of evolutionary change.

> Inbreeding depression can increase the rate at which natural selection removes disadvantageous recessive alleles by exposing these alleles in the homozygous phenotype.

Sexual Selection

> Sexual selection occurs when individuals within a population differ in their ability to attract mates.

> Sexual selection favors individuals with heritable traits that enhance their ability to obtain mates.

> Sexual selection is a special form of natural selection.

> The **fundamental asymmetry of sex** is that females usually invest more in their offspring than males do.

Sexual Selection via Female Choice

Females may choose mates on the basis of:

> physical characteristics that signal male genetic quality

> resources or parental care produced by males

> both physical characteristics and resources or parental care

Sexual Selection via Male–Male Competition

> Sexual selection is intense in elephant seals and is driven by male−male competition.

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> Variation in reproductive success is high in males (Figure 25.14b).

> Females have lower variation in reproductive success (Figure 25.14c).

What Are the Consequences of Sexual Selection?

> Sexually selected traits often differ sharply between the sexes.

> **Sexual dimorphism** refers to any trait that differs between males and females.

> Sexual selection violates the assumptions of the Hardy−Weinberg principle, but causes certain alleles to increase in frequency and results in evolution.

Chapter 26: Speciation

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Key Concepts

> Speciation occurs when populations of the same species become genetically isolated by lack of gene flow and then diverge from each other due to selection, genetic drift, or mutation.

> Populations can be recognized as distinct species if they are reproductively isolated from each other, if they have distinct

morphological characteristics, or if they form independent branches on a phylogenetic tree.

- Populations can become genetically isolated from each other if they occupy different geographic areas, if they use different habitats within the same area, or if one population is polyploid and cannot breed with the other.
- When populations that have diverged come back into contact, several outcomes are possible.

Section 26.1: How Are Species Defined and Identified?

- **Species** are distinct type of organisms and represent evolutionarily independent groups.
- Gene flow eliminated genetic differences among populations, so evolutionary independence starts with lack of gene flow.
- If gene flow between populations stops, then mutation, selection, and drift begin to act on populations independently.
- Allele frequencies and other characteristics of these independent populations diverge and over time the populations can become distinct species.
- Formally, a species is defined as an evolutionarily independent population or group of populations.
- Three criteria for identifying species are in common use:
  –the biological species concept
  –the morphospecies concept
  –the phylogenetic species concept

The Biological Species Concept

- The **biological species concept** considers populations to be evolutionarily independent if they are reproductively isolated from each other.
- No gene flow occurs between these populations.

- **Prezygotic isolation** occurs when individuals of different species cannot mate.
- In this case, reproductive isolation occurs before mating can occur.
- **Postzygotic isolation** occurs when individuals from different populations can mate, but the offspring produced do not survive or produce offspring.
- In this case, interspecies mating does occur, but any hybrid offspring have low fitness.
- The criteria of reproductive isolation can be applied only to populations that overlap geographically.

The Morphogenesis Concept

- Evolutionary independence can also be identified by differences in size, shape, or other morphological features.

- Distinguishing features are most likely to arise if populations are independent and isolated from gene flow.
- This **morphospecies concept** can be applied easily but is rather subjective.

The Phylogenetic Species Concept

- The **phylogenetic species concept** is based on reconstructing the evolutionary history of populations.
- On phylogenetic trees, an ancestral population plus all its descendants is called a **monophyletic group.**
- A species is defined as the smallest monophyletic group on a tree; by definition, it is isolated from gene flow with other groups.
- On a phylogenetic tree of populations, each tip is a phylogenetic species.
- The **phylogenetic species concept** can be applied to any population.
- This concept is logical because populations are distinct enough to be monophyletic only if they are isolated from gene flow and have evolved independently.
- In practice, biologists use all three species concepts.

Species Definitions in Action: The Case of the Dusky Seaside Sparrow

- **Subspecies** are populations that live in discrete geographic areas and have their own identifying traits but are not distinct enough to be considered a separate species.
- Seaside sparrow subspecies are physically isolated from one another, and it was believed that there was little or no gene flow between populations.

- Based on the biological species concept and the morphospecies concept, these subspecies would be considered species.
- Phylogenetic analysis of gene sequences from different seaside sparrow populations showed that only two species of seaside sparrows exist.
- One subspecies thought to be nearing extinction was shown to be genetically indistinguishable from the sparrows and thus did not need to be individually preserved.

Section 26.2: Isolation and Divergence in Allopatry

- Genetic isolation happens routinely when populations become physically separated.
- Physical isolation occurs by dispersal or vicariance.
- Dispersal is when a population moves to a new habitat, colonizes it, and forms a new population.
- Vicariance is a physical splitting of a habitat, as when a physical barrier splits a widespread population into subgroups that are physically isolated from each other.
- Speciation that begins with physical isolation via either dispersal or vicariance is known as **allopatric speciation**.

- Populations that live in different areas are said to be in **allopatry**.
- **Biogeography**—the study of how species and populations are distributed geographically—can tell us how colonization and range–splitting events occur.

Dispersal and Colonization Isolate Populations

- Colonization events often cause speciation because the physical separation reduces gene flow and genetic drift will cause the old and new populations to diverge rapidly.
- Drift occurs during the colonization event via the founder effect.
- Natural selection may cause divergence if the newly colonized environment is different from the original habitat.
- The characteristics of a colonizing population are likely to be different from the characteristics of the source population due to founder effects.
- Subsequent natural selection may extend the rapid divergence that begins with genetic drift.
- Colonization, followed by genetic drift and natural selection, is thought to be responsible for speciation in many island groups.

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Vicariance Isolates Populations

- When an existing population is split by a new physical barrier, vicariance has occurred.
- The last ice age caused vicariance as a result of glaciation, which created physical barriers.
- In addition, **continental drift**—the movement of continental plates explained by the **theory of plate tectonics**—separated species physically.
- Physical isolation of populations via dispersal or vicariance produced genetic isolation, the first requirement of speciation.
- When genetic isolation is accompanied by genetic divergence due to mutation, selection, and genetic drift, speciation results.

Section 26.3: Isolation and Divergence in Sympatry

- Populations or species that live in the same geographic region (close enough to mate) live in **sympatry**.
- Researchers used to think that speciation could not occur among sympatric populations because gene flow is possible.
- Gene flow should eliminate evolutionary differences among populations created by genetic drift and natural selection.

Can Natural Selection Cause Speciation Even When Gene flow Is Possible?

- Under certain circumstances, natural selection can overcome gene flow and natural selection and cause **sympatric speciation**.
- Even though populations are not physically isolated, they may be isolated by preferences for different habitats.

> The soapberry bug is a species of insect that feeds on certain plants and mate on their host plant.
> Soapberry bugs began to use new species of plants that were introduced to their environment as food.
> The fruits of nonnative plant species are much smaller than those of the native plant species.
> Soapberry bug populations that feed on the two host plants were found to have very different beak lengths, which correspond to differences in the size of the host fruit.

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> This switch to a new host species should reduce gene flow and set up disruptive selection.
> As a result, natural selection may be able to overwhelm gene flow and cause speciation even when populations are sympatric.

How Can Polyploidy Lead to Speciation?

> Although mutation is the ultimate source of genetic variation in populations, it is an inefficient evolutionary mechanism.
> However, a mutation that results in **polyploidy**—the condition of having more than two sets of chromosomes—can cause speciation, particularly in plants.
> Polyploidy reduces gene flow between mutant and normal individuals.
> Polyploid individuals are genetically isolated from wild type individuals because they produce diploid gametes rather than haploid gametes.
> A resulting zygote would be triploid. Triploid individuals produce gametes with a dysfunctional set of chromosomes.
> Mutations that result in a doubling of chromosome number produce **autopolyploid** individuals.
> In these individuals, the chromosomes all come from the same species.
> **Allopolyploid** individuals are created when parents that belong to different species mate and produce an offspring where chromosome number doubles.
> These individuals have chromosome sets from different species.

Autopolyploidy

–Because polyploids are genetically isolated and thus evolutionarily independent, genetic drift and selection may cause the wild type and polyploid populations to diverge.

–Speciation is then underway.

Allopolyploidy

–Allopolyploidy may occur after two species hybridize (Figure 26.10).

–Many hybrid offspring are sterile because their chromosomes do not pair normally during meiosis.

–However, if a mutation occurs that doubles the chromosome number, then homologs synapse normally and gametes can be produced.

–These gametes may be able to self–fertilize to produce a tetraploid offspring.

–Many diploid plant species have closely related polyploid species.

–This backs the claim that speciation by polyploidization is important in plants.

–Speciation by polyploidization is driven by chromosome–level mutations and occurs in sympatry.

Section 26.4: What Happens When Isolated Populations Come into Contact?

> If two populations have diverged and if divergence has affected when, where, or how individuals in the populations mate, it is unlikely that interbreeding will take place.

> In cases such as this in which prezygotic isolation exists, mating between the populations is rare, gene flow is minimal, and the populations continue to diverge.

> When prezygotic isolation does not occur, populations may successfully interbreed.

> Gene flow then occurs and may erase distinctions between the two populations.

> Other possible outcomes are reinforcement, hybrid zones, and speciation by hybridization.

Reinforcement

> If two populations have diverges extensively and distinct genetically, their hybrid offspring will most likely have lower fitness and will not develop or reproduce normally.

> This is a case of postzygotic isolation.

> Postzygotic isolation causes natural selection against interbreeding.

> Selection for traits that isolate populations reproductively is called **reinforcement.**

> Sympatric species living in the same area are seldom willing to mate with one another.

> Allopatric species living in different areas are often willing to mate with one another.

–This is the pattern expected by reinforcement.

Hybrid Zones

> Sometimes hybrid offspring possess traits that are intermediate between the two parental populations and are healthy and capable of breeding.

> A geographic area where interbreeding between the two populations is

common and there are lots of hybrid offspring is called a **hybrid zone**

> An example of this is seen with warblers.

–Hybridization often leads to extinction but sometimes leads to creation of a new species.

New Species through Hybridization

> New species can originate by hybridization events, as demonstrated by sunflower species.

> Experimental evidence provides strong support for creation of new species by hybridization.

> There are a number of outcomes of secondary contact of two populations:

–fusion of the populations
–reinforcement of divergence
–founding of stable hybrid zones
–extinction of one population
–creation of a new species

Chapter 27:Phylogenies and the History of Life

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Key Concepts

> Phylogenies and the fossil record are the major tools that biologists use to study the history of life.

> The Cambrian explosion was the rapid morphological and ecological diversification of animals that occurred during the Cambrian period.

> Adaptive radiations are a major pattern in the history of life. They are instances of rapid diversification associated with new ecological opportunities and new morphological innovations.

> Mass extinctions have occurred repeatedly throughout the history of life. They rapidly eliminate most of the species alive in a more or less random manner.

Section 27.1: Tools for Studying History: Phylogenetic Trees

> The evolutionary history of a group of organisms is called a **phylogeny**.

> A **phylogenetic tree** shows ancestor–descendant relationships among populations or species.

Reading Phylogenetic Trees

> **Branches** represent populations through time. Adjacent branches are **sister taxa** (a **taxon** is any named group of organisms).

> **Nodes** occur where an ancestral group split into two or more descendant groups.

> A **polytomy** is a node where more than two descendant groups branch off.

> **Tips** are the tree's endpoints and represent living groups or a group’s end in extinction.

> In **rooted** phylogenies the most ancient node of the tree is shown at the

bottom.
> The location of this node is determined using an **outgroup**, a taxonomic group that diverged before the rest of the taxa being studied.
> An ancestor and all its descendants form a **monophyletic group** (also called a **clade** or **lineage**).

How Do Researchers Estimate Phylogenies?

> Morphological and/or genetic characteristics are used to estimate phylogenetic relationships among species.
> The **phenetic approach** to estimating trees is based on the overall similarity among populations.

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> A tree is built that clusters the most similar populations and places more divergent populations on more distant branches.
> The **cladistic approach** to inferring trees focuses on **synapomorphies**, the shared derived characters of the species under study.
> A synapomorphy is a trait that certain populations or species have that exists in no others.
> When many such traits have been measured, traits unique to each monophyletic group are identified and the groups are placed on a tree in the correct relationship to one another.

How Can Biologists Distinguish Homology from Homoplasy?

> Problems can arise with both cladistic and phenetic analysis because similar traits can evolve independently in two distant species rather than from a trait present in a common ancestor.
> **Homoplasy** occurs when traits are similar for reasons other than common ancestry.
> **Homology** occurs when traits are similar due to shared ancestry.
> **Convergent evolution** occurs when natural selection favors similar solutions to the problems posed by a similar way of making a living.
> Convergent evolution is a common cause of homoplasy.
> If similar traits found in distantly related lineages are indeed similar due to common ancenstry, then similar traits should be found in many intervening lineages on the tree of life.
> **Parsimony** is a principle of logic stating that the most likely explanation or pattern is the one that implies the least amount of change.
> Convergent evolution and other causes of homoplasy should be rare compared with similarity due to share descent, so the tree that implies the fewest overall evolutionary changed should be the one that most accurately reflects what really happened during evolution.

Whale Evolution: A Case History

> Traditionally, phylogenetic trees based on morphological data place whales outside of the artiodactyls—mammals that have hooves, an even number of toes, and an unusual pulley–shaped ankle bone (astralagus).

> DNA sequence data, however, suggest a close relationship between whales and hippos.

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> Recent data on short interspersed nuclear elements (SINEs) show that whales and hippos share several SINE genes that are absent in other artiodactyl groups.

> These SINEs are shared derived traits (synapomorphies) and support the hypothesis that whales and hippos are indeed closely related.

Section 27.2: Tools for Studying History: The Fossil Record

> The fossil record provides the only direct evidence about what organisms that lived in the past looked like, where they lived, and when they existed.

> A **fossil** is the physical trace left by an organism that lived in the past.

> The **fossil record** is the total collection of fossils that have been found throughout the world.

How Do Fossils Form?

> Most fossils form when an organism is buried in sediment before decomposition occurs.

> Four types of fossils are intact fossils, compression fossils, cast fossils, and premineralized fossils.

> Fossilization is an extremely rare event.

Limitations of the Fossil Record

> There are several features and limitations of the fossil record that must be recognized: habitat bias, taxonomic bias, temporal bias, and abundance bias.

> Habitat bias occurs because organisms that live in areas where sediments are actively being deposited are more likely to form fossils than are organisms that live in other habitats.

> Taxonomic bias is due to the fact that some organisms (e.g., those with bones) are more likely to decay slowly and leave fossil evidence.

> Temporal bias occurs because more recent fossils are more common than ancient fossils.

> Abundance bias occurs because organisms that are abundant, widespread, and present on Earth for a long time leave evidence much more often than do species that are rare, local, or ephemeral.

> **Paleontologists**—scientists who study fossils—recognize that they are limited to asking questions about tiny and scattered segments on the tree of life.

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> Yet analyzing fossils is the only way scientists have of examining the physical appearance of extinct forms and inferring how they lived.

Life's Timeline

- Major events in the history of life are marked on the timeline which has been broken into four segments (the Precambrian, the Paleozoic, the Mesozoic, and the Cenozoic).
- The **Precambrian era** encompasses the **Hadean**, **Archaean**, and **Proterozoic eons.**
- In the Precambrian era, almost all life was unicellular and hardly any oxygen was present.
- Many animal groups—including fungi, land plants, and land animals—appeared in the **Paleozoic era.**
- The **Mesozoic era**, also known as the Age of Reptiles, ended with the extinction of the dinosaurs.
- The **Cenozoic era** is known as the Age of Mammals.

Section 27.3: The Cambrian Explosion

- Animals first originated around 565 million years ago (Mya).
- Soon after that, animals diversified into almost all the major groups extant today.
- This is known as the **Cambrian explosion.**

Cambrian Fossils: An Overview

- The Cambrian explosion is documented by three major fossil assemblages
- The presence of these exceptionally rich deposits before, during, and after the Cambrian explosion makes the fossil record for this event extraordinarily complete.

The Doushantuo Microfossils

- Researchers identified sponges, cyanobacteria, and multicellular algae in samples dated 570–580 Mya. They also found what they concluded were animal embryos in early stages.

The Edicaran Faunas

- Sponges, jellyfish, comb jellies, and traces of other animals dated 544–565 Mya are found in fossils from the Ediacara Hills of Australia.

The Burgess Shale Faunas

- Virtually every major animal group is represented in the Burgess Shale fossils, which date 525–515 Mya.

- These fossils indicated a tremendous increase in the size and morphological complexity of animals, accompanied by diversification in how they made a living.

Did Gene Duplication Trigger the Cambrian Explosion?

- Many researchers predicted there would be a strong association between the order in which animal lineages appeared during evolutionary history, the number of Hox genes present in each lineage, and each lineage's morphological complexity and body size.
- A phylogenetic tree of Hox genes in animals in general support this

hypothesis

> The following conclusions can be made from this phylogeny:

–the number of genes in the Hox cluster appears to have expanded during the course of evolution

–Hox genes appear to have been created by gene duplication events because the genes within the cluster are similar in structure and base sequence

–the entire Hox cluster was duplicated and then duplicated again in the lineage leading to vertebrates

> Duplication of Hox genes has been important in making the elaboration of animal body plans possible.

> However, changes in expression and function of existing genes have been equally or even more important.

Section 27.4: Adaptive Radiations

> One broad pattern that can be observed in the tree of life is that dense groups of branches are scattered throughout the tree.

> These star phylogenies represent major diversification over a relatively short period of time, a process known as **adaptive radiation.**

> The Cambrian explosion can be considered an extremely large–scale adaptive radiation.

Ecological Opportunity as a Trigger

> One of the most consistent themes in adaptive radiations is ecological opportunity.

> Biologists have documented adaptive radiations of the Anolis lizards of the Caribbean islands

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> On the two islands studied, the same four ecological types eventually evolved, because the islands had similar varieties of habitats.

Morphological Innovation as a Trigger

> Adaptive radiation is usually associated with a new ecological opportunity or morphological innovation.

> After adaptive radiation, rapid speciation and morphological divergence are tightly linked.

> Web animation – Adaptive radiation

Section 27.5: Mass Extinctions

> A **mass extinction** is the rapid extinction of a large number of lineages scattered throughout the tree of life.

> A mass extinction occurs when at least 60% of the species present are wiped out within 1 million years.

> Mass extinctions are caused by catastrophic episodes.

> Paleontologists traditionally recognize five mass extinctions ("The Big Five").

> **Background extinction** is the lower, average rate of extinction, representing the normal loss of some species that always occurs.

How Do Background and Mass Extinctions Differ?

> Background extinctions typically occur when normal environmental change, emerging diseases, or competition reduces certain populations to zero.

> Mass extinctions result from extraordinary, sudden, and temporary changes in the environment.

> During a mass extinction, species do not die out due to poor adaptation. Instead, species die out from exposure to exceptionally harsh, short–term conditions.

> Natural selection causes most background extinctions, whereas mass extinctions function like genetic drift.

What Killed the Dinosaurs?

> The **impact hypothesis** for the extinction of dinosaurs proposed that an asteroid struck Earth and snuffed out an estimated 60–80% of the multicellular species alive.

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> Conclusive evidence—including iridium, shocked quartz, and microtektites found in rock layers dated to 65 million years ago, as well as a huge crater off the —has led researchers to accept the impact hypothesis.

Selectivity

> Some evolutionary lineages were better able than others to withstand the environmental change brought on by the asteroid impact.

> Why certain groups survived while others perished is still a mystery.

Recovery

> Ferns appear to have replaced diverse woody and flowering plants in many habitats following the K–T extinction.

> Mammals diversified to fill the niches left empty following the dinosaur extinctions.

Chapter 50: An Introduction to Ecology

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Key Concepts

> Ecology focuses on how organisms interact with their environment. Because its goal is to understand the distribution and abundance of organisms, ecology provides a scientific foundation for the conservation of species and natural areas.

> Physical structure—particularly water depth—is the primary factor that limits the distribution and abundance of aquatic species. Climate—specifically, both the average value and annual variation in temperature and in moisture—is the primary factor that limits the distribution and abundance of terrestrial species.

> Climate varies with latitude, elevation, and other factors. Climate is changing rapidly around the globe.

> In addition to abiotic aspects of the environment such as physical structure and climate, species distribution is constrained by historical and biotic factors.

Section 50.1: Areas of Ecological Study

In ecology, researchers work at four main levels: organisms, populations, communities, and ecosystems.

Organismal Ecology

> Organismal ecologists explore the morphological, physiological, and behavioral adaptations that allow individual organisms to live successfully in a particular area.

Population Ecology

> A **population** is a group of individuals of the same species that live in the same area at the same time.

> Population ecologists focus on how the numbers of individuals in a population change over time.

Community Ecology

> A biological **community** consists of the species that interact with one another within a particular area.

> Community ecologists study the nature and consequences of the interactions among species in a community.

Ecosystem Ecology

> An **ecosystem** consists of all the organisms in a particular region, along with nonliving, or **abiotic**, components.

> Ecosystem ecologists study how nutrients and energy move among organisms and between organisms and the surrounding atmosphere and soil or water.

How Do Ecology and Conservation Efforts Interact?

Conservation biology—the effort to study, preserve, and restore threatened populations, communities, and ecosystems—synthesizes and applies the four levels of ecological study.

> Conservation biologists prescribe remedies for threatened species and manage land to produce a diversity of species, clean air, pure water, and productive soils.

Section 50.2: Types of Aquatic Ecosystems

> An organism’s environment has both physical and biological components.

> The abiotic components include temperature, precipitation, wind, and sunlight.

> The biotic (living) components consist of other members of the organism’s own species as well as individuals of other species.

What Physical Factors Play a Key Role in Aquatic Environments?

- Water depth and the rate of water movement qualify as the key physical factors that shape the environments in aquatic ecosystems.
- Water depth dictates how much light reaches the organisms that live in a particular region. The amount and types of wavelengths available to organisms change dramatically as water depth increases.
- The type and amount of water flow also have a major influence in aquatic environments.
- Organisms that live in fast–flowing streams, for example, must cope with the physical force of the water, which constantly threatens to move them downstream.

Freshwater Environments – Lakes and Ponds

- Lakes and ponds are distinguished by size—ponds are smaller than lakes.
- Lakes and ponds have five zones:

–The **littoral zone** consists of the shallow waters along the shore, where flowering plants are rooted.

–The **limnetic zone** is offshore and comprises water that receives enough light to support photosynthesis.

–The **benthic zone** is made up of the substrate

–Regions of the littoral, limnetic, and benthic zones that receive sunlight are part of the **photic zone**.

–Portions of the lake or pond that do not receive sunlight make up the **aphotic zone**.

- Water movement in lakes and ponds is driven by wind and temperature.
- The littoral and limnetic zones are typically much warmer and better oxygenated than the benthic zone.
- The benthic zone is relatively nutrient rich because dead and decomposing bodies accumulate there.
- Plankton and fish live in the photic zone.
- Animals that consume **detritus** (dead organic matter) are common in the benthic zone.

Freshwater Environments – Wetlands

- **Wetlands** are shallow–water habitats where the soil is saturated with water for at least part of the year.
- Wetlands have only shallow water and have **emergent vegetation**—plants that grow above the surface of the water.
- Wetland types are distinguished by water flow and vegetation.
- **Bogs** develop in depressions where water flow is low or absent.
- Most of the water in bogs is stagnant, so oxygen is used up by the decomposition of dead organic matter faster than it enters by diffusion from the atmosphere. As a result, bog water is oxygen–poor or even anoxic, making bogs remarkably unproductive.

> **Marshes** lack trees and typically feature grasses. They offer ample supplies of oxygenated water and sunlight, and are extraordinarily productive.

> **Swamps** are similar to marshes but are dominated by trees and shrubs. Like marshes, swamps offer ample supplies of water and sunlight, and are extraordinarily productive.

Freshwater Environments – Streams

> **Streams** are bodies of water that move constantly in one direction.

> Creeks are small streams, rivers are large.

> The structure of a typical stream varies along its length (Figure 50.6).

> As a result, the same stream often contains completely different types of organisms near its source and near its end.

Freshwater/Marine Environments – Estuaries

> An **estuary** forms where a river meets the ocean and freshwater mixes with salt water.

> Species that live in estuaries have adaptations that allow them to cope with variations in salinity.

> Because the water is shallow and sunlit, and because nutrients are constantly replenished by incoming river water, estuaries are among the most productive environments.

Marine Environments – the Oceans

> The ocean has six regions:

–The **intertidal zone** consists of a rocky, sandy, or muddy beach that is exposed to the air at low tide but submerged at high tide.

–The **neritic zone** extends from the intertidal zone to depths of about 200 m. Its outermost edge is defined by the end of the **continental shelf**—the gently sloping, submerged portion of a continental plate.

–The **oceanic zone** is the open ocean – the deepwater region beyond the continental shelf.

–The bottom of the ocean is the **benthic zone.**

–The intertidal and sunlit regions of the neritic, oceanic, and benthic zones make up a **photic zone**.

–Areas that do not receive sunlight are in an **aphotic zone**.

> Water movement in the ocean is dominated by different processes at different depths.

> Tides and wave action are the major influences in the intertidal zone.

> In the neritic zone, currents have a heavy impact.

> Each zone in the ocean is populated by distinct species that are adapted to the physical conditions present.

Section 50.3: Types of Terrestrial Ecosystems

> **Biomes** are major groupings of plant and animal communities defined by

a dominant vegetation type.
> Each biome is associated with a distinctive set of abiotic conditions.
> The type of biome present in a terrestrial region depends on **climate**, the prevailing, long–term weather conditions found in an area.
> **Weather** consists of the specific short–term atmospheric conditions of temperature, moisture, sunlight, and wind.

> The nature of the biome that develops in a particular region is governed by the average annual temperature and precipitation, and the annual variation in temperature and precipitation.
> Each biome contains species that are adapted to a particular temperature and moisture regime.
> **Net primary productivity (NPP)** is the total amount of carbon that is fixed per year minus the amount of fixed carbon oxidized during cellular respiration.
> NPP represents the organic matter that is available as food for other organisms.
> In terrestrial environments NPP is often estimated by measuring **aboveground biomass**, the total mass of living plants, excluding roots.

Terrestrial Biomes – Tropical Wet Forests

> Tropical wet forests, or rain forests, are found in equatorial regions where temperatures and rainfall are high and annual variation is low.
> The favorable year–round growing conditions produce riotous growth, leading to extremely high and aboveground biomass.
> Tropical wet forests are renowned for their species diversity. The diversity of plant sizes and growth forms produces extraordinary structural diversity.
> A tree **canopy** (the uppermost layers of branches) is intermingled with vines, **epiphytes** (plants that grow entirely on other plants), shrubs, and herbs.
> The diversity of growth forms presents a variety of habitat types for animals.

Terrestrial Biomes – Subtropical Deserts

> Subtropical deserts are characterized by high average annual temperatures, moderate variation in temperature, and very low precipitation.
> The scarcity of water in subtropical deserts has profound implications. Because conditions are rarely favorable enough to support photosynthesis, the productivity of desert communities is very low.
> Desert species adapt to the extreme temperatures and aridity by growing at a low rate year–round or by breaking dormancy and growing rapidly in response to any rainfall.

Terrestrial Biomes – Temperate Grasslands

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> **Temperate** regions have moderate temperatures relative to the tropics and polar regions; summers are typically long and warm, winters short and cold.

> Temperature variation is important because it dictates a well–defined growing season.

> In the temperate zone, plant growth is possible only in spring, summer, and fall months when moisture and warmth are adequate.

> Grasses are the dominant life–form in temperate regions with relatively low rainfall.

> Although the productivity of temperate grasslands is generally lower than that of forest communities, grassland soils are often highly fertile.

Terrestrial Biomes – Temperate Forests

> In temperate areas with relatively high precipitation, grasslands give way to forests.

> Temperate forests experience a period in which mean monthly temperatures fall below freezing and plant growth stops.

> Unlike grassland climates, precipitation is moderately high and relatively constant throughout the year.

> Most temperate forests have productivity levels that are lower than those of tropical forests but higher than those of deserts and grasslands. The level of diversity is also moderate.

Terrestrial Biomes – Boreal Forests

> The boreal forest, or **taiga**, stretches across most of Canada, Alaska, Russia, and northern Europe.

> The climate is characterized by very cold winters and short, cool summers. Temperature variation is extreme.

> Annual precipitation is low, but temperatures are so cold that evaporation is minimal. As a result, moisture is usually abundant enough to support tree growth.

> Boreal forests are dominated by highly cold–tolerant conifers, including spruce, pine, fir, and larch.

> The productivity of boreal forests is low, but aboveground biomass is high because slow–growing tree species may be long–lived and gradually accumulate large standing biomass.

> Boreal forests also have exceptionally low species diversity.

Terrestrial Biomes – Arctic Tundra

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> The arctic **tundra** has very low temperatures with high annual temperature variation and very low annual precipitation.

> The growing season is 6–8 weeks at most; temperatures are below

freezing the rest of the year.

> The arctic tundra is treeless except for small woody shrubs.

> Arctic tundra has low plant species diversity, low productivity, and low aboveground biomass.

> Most tundra soils are in the perennially frozen state known as **permafrost.** The low temperatures inhibit both the release of nutrients from decaying organic matter and the uptake of nutrients into live roots.

> Animal diversity also tends to be low.

Section 50.4: The Role of Climate and the Consequences of Climate Change

> Each type of aquatic environment and terrestrial biome hosts species that are adapted to the abiotic conditions present at the location.

> Global warming is having a profound impact on these abiotic factors.

Why Are the Tropics Warm and the Poles Cold?

> Areas of the world are warm if they receive a large amount of sunlight per unit area; they are cold if they receive a small amount of sunlight per unit area.

> Earth's shape dictates that regions at or near the equator receive more sunlight per unit area than regions that are closer to the poles.

Why Are the Tropics Wet?

> Areas along the equator receive the most moisture; locations at about 30 degrees latitude north and south of the equator are among the driest on Earth.

> A major cycle in global air circulation, called a **Hadley cell**, is responsible for this pattern.

> Air heated by the strong sunlight along the equator expands and rises. Warm air can hold a great deal of moisture because warm water molecules tend to stay in vapor form instead of condensing into droplets.

> As the air rises, it radiates heat to space and begins to cool. As it cools, its ability to hold water declines, water condenses, and high levels of precipitation occur along the equator.

> As more air is heated along the equator, the cooler, older air above Earth's surface is pushed poleward.

> As the air mass cools, its density increases and it begins to sink. As it sinks, it absorbs more and more solar radiation from Earth's surface and begins to warm, gaining water–holding capacity.

> The result is a band of deserts near 30° latitude north and south.

What Causes Seasonality in Weather?

> Seasons—regular, annual fluctuations in temperature, precipitation, or both—result from Earth's 23.5º tilt on its axis

> In June, the Northern Hemisphere is tilted toward the Sun, faces the Sun most directly, and receives the largest amount of solar radiation per unit area.

- In December, the Southern Hemisphere is tilted toward the Sun, faces the Sun most directly, and receives the largest amount of solar radiation per unit area.
- Thus, summer is in June in the Northern Hemisphere and in December in the Southern Hemisphere.
- In March and September, the equator faces the Sun most directly, so the tropics receive the most solar radiation.

Mountains and Oceans: Regional Effects on Climate

- Mountains and oceans cause regional effects on climate.
- The presence of mountain ranges tends to produce extremes in precipitation.
- Oceans have a moderating influence on temperature.
- Oceans have a moderating influence on temperature.
- Water can absorb a great deal of heat from the atmosphere in summer, when the water temperature is cooler than the air temperature, so the ocean moderates summer temperatures on nearby landmasses.
- The ocean releases heat to the atmosphere in winter, when the water temperature is warmer than the air temperature, so islands and coastal areas have much more moderate climates than do nearby inland areas.

How Will Global Warming Affect Ecosystems?

- Climate has a dramatic effect on both terrestrial and aquatic ecosystems.
- Biologists use three tools to predict how global warming will affect aquatic and terrestrial ecosystems: simulation studies, observational studies, and experiments.

Experiments That Manipulate Temperature

- Experimental increases in temperature have been shown to change species composition in arctic tundra.
- These results support simulation and observational studies predicting that arctic tundra environments are giving way to boreal forest.

Experiments That Manipulate Precipitation

- Simulation and observational studies indicate that global warming is making climates more extreme.
- Experimental increases in rainfall variability have been shown to change species composition in temperate grasslands (Figure 50.28).

Section 50.5: Biogeography: Why Are Organisms Found Where They Are?

- **Biogeography** is the study of how organisms are distributed geographically.
- The **range**, or geographical distribution, of every species on Earth is limited – no organism can live everywhere.

The Role of History

- To understand why certain species occur in a particular region and others don’t, the first factor to consider is history—specifically, the history of dispersal.

> **Dispersal** is the movement of an individual from its place of birth to the location where it lives and breeds as an adult.

> If an **exotic** species is introduced into a new area, spreads rapidly, and eliminates native species, it is considered an **invasive species**.

> Data show that only about 10% of the species introduced to an area actually become common, and a smaller percentage increases in population enough to be considered invasive.

Biotic Factors

> The distribution of a species is often limited by biotic factors—interactions with other organisms.

> For example, distribution of cattle is limited by distribution of tsetse flies in Africa.

Abiotic Factors

> The distribution of species can also be limited by abiotic factors, particularly temperature and moisture. An area may simply be too cold or too dry for a particular organism to survive.

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> It is often difficult to separate the effects of biotic and abiotic factors on species' range.

Chapter 51: Behavior

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Key Concepts

> After describing a behavior, biologists seek to explain both its proximate and ultimate causes—meaning, how it happens at the genetic and physiological levels and how it affects the individual's fitness.

> In a single species, behavior may range from highly stereotyped, invariable responses to highly flexible, conditional responses and from unlearned to learned responses.

> The types of learning that individuals do, the way they communicate, and the way they orient and navigate all correlate closely with their habitat and with the challenges they face in trying to survive and reproduce.

> When individuals behave altruistically, they are usually helping close relatives or individuals that help them in return.

Section 51.1: Types of Behavior: An Overview

> Some types of behavior are performed in nearly the same way every time. Other types of behavior are highly flexible.

> **Learning** is a change in behavior that results in a specific experience in the life of an individual.

> Some types of behavior are readily modified by learning, others are not.

Innate Behavior

> **Fixed action patterns** (**FAPs**) are highly stereotypical behavior patterns

that are usually triggered by simple stimuli called **releasers** or **signal stimuli**.

> FAPs are examples of innate behavior, behavior that is inherited and shows little variation based on learning or the individual's behavior.

> It is common to observe innate behavior in response to: (1) situations that have a high impact on fitness and demand a reflex–like, unlearned response, and (2) situations where learning is not possible.

Conditional Strategies and Decision Making

> Although all species show some degree of innate behavior, it is much more common for an individual's behavior to change in response to learning and to show flexibility in response to changing environmental conditions.

> Animals take in information about their environment and weigh the costs and benefits of responding in various ways.

What Decisions Do White–Fronted Bee–Eaters Make When Foraging?

> Biologists assume that animals will choose to optimize their feeding efficiency, called **optimal foraging**.

> White–fronted bee–eaters vary their foraging behavior depending on conditions.

How Do Female Barn Swallows Choose Mates?

> Although both male and female barn swallows help build the nest and feed the young, the species exhibits a significant amount of sexual dimorphism.

> Female barn swallows were found to prefer long–tailed mates.

> Long–tailed males are more efficient in flight and more successful in finding food, and thus have higher fitness.

Why Do Some Bluehead Wrasses Undergo a Sex Change?

> The size–advantage hypothesis states that if a group of fish are living in a territory dominated by a single male, and if that male dies, then females should switch from female to male if their body size is very large.

> This change is costly in terms of time and energy, but the benefit is large since that female can increase her number of offspring as a male fertilizing eggs as compared to a female laying eggs.

> In many cases, animals have alleles that make a wide range of behavior possible; what an individual actually does is based on decisions that change, depending on conditions.

Section 51.2: Learning

> Learning occurs when behavior changes in response to specific life experiences. It is particularly important in species that have large brains and a lifestyle dominated by complex social interactions. In such species, FAPs and other types of inflexible, stereotyped behaviors are relatively rare. Instead, each individual is capable of a wide range of

behavior.

Simple Types of Learning: Classical Conditioning and Imprinting

> In **classical conditioning**, individuals are trained by experience to give the same response to more than one stimulus—even a stimulus that has nothing to do with the normal response.

> Upon hatching, ducklings and goslings adopt as their mother the first moving thing they see.

> This type of learning is called **imprinting**. It is fast and irreversible and occurs only during a short **critical** or **sensitive period**.

> Recent research has shown that the ability of humans to learn a particular language shares at least some of the characteristics of imprinting.

More Complex Types of Learning: Birdsong

> Song–learning behavior is innate in certain species and may be highly stereotyped.

> Depending on the species, song–learning behavior falls at various locations on the learning continuum.

> In some species, singing must be learned during a certain critical period and occurs only in response to certain types of stimuli (Figure 51.8).

> Singing in white–crowned sparrows is heavily influenced by learning, but learning is constrained to certain periods of life and occurs only in response to certain types of stimuli.

Can Animals Think?

> **Cognition** is the recognition and manipulation of facts about the world and the ability to form concepts and gain insights.

> New Caledonian crows can make tools and solve complex problems, which suggests that they can think (Figure 51.9).

> This crows–can–think hpothesis is supported by experimental evidence.

What Is the Adaptive Significance of Learning?

> Several types of learning exist, and the ability to learn varies widely among species.

> Learning is an adaptation that helps organisms cope with challenges from their environment.

Section 51.3: How Animals Act: Hormonal and Neural Control

> Most behavior is modified at least slightly by some type of learning, and most animals have behavioral responses that range from highly stereotyped to highly flexible.

> When behavior is flexible and condition dependent, it means that an individual has the potential to behave in a variety of ways.

Sexual Activity in Anolis Lizards

> Sexual activity in Anolis lizards provides an example of how changes in behavior are implemented and controlled.

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> A series of experiments showed that sexual activity in Anolis lizards is a condition–dependent behavior controlled by hormones.

> Two types of stimulation are necessary to produce the hormonal changes that lead to sexual behavior. Females need to experience springlike light and temperatures and exposure to breeding mates.

Escape Behavior in Noctuid Moths

> Bats find insects in the dark by echolocation.

> Noctuid moths can hear the sounds bats use for echolocation and respond differently to it depending on how far away the bat is.

Section 51.4: Communication

> **Communication** is a process in which a **signal** (any information–containing behavior) from one individual modifies the behavior of another individual.

> Communication is a social process.

> For communication to occur, it is not enough that a signal be sent; the signal also must be received and acted on.

Modes of Communication

> Communication can be acoustic, visual, olfactory, or tactile. The type of signal an organism uses correlates with its habitat.

> It is common to observe several modes of communication being used in conjunction.

> For example, visual and auditory stimuli are important in territorial behavior in red–winged blackbirds.Each type of stimulus alone induces a response, but the combination of both stimuli provokes a more powerful change in behavior.

> Each mode of communication has advantages and disadvantages. Communication systems have been honed by natural selection to maximize their costs.

A Case History: The Honeybee Dance

> Karl von Frisch suspected that honeybees that are successful in finding food communicate the location of food to other honeybees.

> He observed bees displaying a "round dance" to workers that contained information about the location of food.

> He also observed a "waggle run" that gave information about the distance the workers must fly, as well as the direction.

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> Both the round dance and the waggle dance communicate information about food sources.

> The orientation of the waggle dance varied and the variation correlated with the direction of the food source from the hive, and the length of the

straight waggling run was proportional to the distance the foragers had to fly to reach the feeder.

> These dances communicated the position of the food relative to the current position of the sun.

When Is Communication Honest or Deceitful?

> In some cases, it is advantageous for an individual to convey information accurately.

> In other cases, natural selection has favored the evolution of deceitful communication, or lying.

Deceiving Individuals of Another Species

> Individuals increase their fitness by providing inaccurate or misleading information to members of a different species

Deceiving Individuals of the Same Species

> In some cases, natural selection has also favored the evolution of traits or actions that deceive members of the same species.

> A male bluegill will mimic a female—he looks like a female and even acts like a female during courtship movements with territory–owning males. The territory–owning male thinks he is courting two females.

> When the actual female begins to lay eggs, the mimic releases sperm and fertilizes some of the eggs. The female–mimic male fathers offspring but does not help care for them.

When Does Deception Work?

> Lying works only when it is relatively rare. If deceit becomes common, natural selection will strongly favor individuals that can detect and avoid or punish liars.

Section 51.5: Migration and Navigation

> In a response to many stimuli, organisms move.

> A movement that results in a change of position is called **orientation**.

> The simplest type of orientation is called **taxis**—the positioning of the body, or part of the body, toward or away from a stimulus.

> Positive **phototaxis** is an orientation toward light.

> Positive **phonotaxis** is an orientation toward sound.

Why Do Animals Move with a Change of Seasons?

> In ecology, **migration** is defined as the long–distance movement of a population associated with a change of seasons.

> At the ultimate level, migration exists because individuals that migrate achieve higher reproductive success than individuals that do not migrate.

> At the proximate level, explaining migratory movements is often extremely difficult.

How Do Animals Find Their Way?

> Biologists distinguish three categories of navigation:

> **Piloting** is the use of familiar landmarks.

> **Compass orientation** is movement oriented in a specific direction.
> **True navigation** is the ability to locate a specific place on Earth's surface.

Piloting

> Many species use piloting to find their way. In some species of migratory birds and mammals, offspring seem to memorize the route by following their parents south in the fall and north in the spring.

Compass Orientation

> Birds and perhaps other organisms have multiple mechanisms for finding a compass direction.
> At least some species can use a Sun compass, a star compass, and a magnetic compass. Which system they use depends on the weather and other circumstances.
> Most animals have a **circadian clock** that maintains a 24–hour rhythm of chemical activity. The clock is set by the light–dark transitions of day and night and tells an animal enough about the time of day that it can use the Sun’s position to find magnetic north.
> On clear nights, migratory birds in the Northern Hemisphere can use the North Star to find magnetic north.
> During cloudy weather, birds appear to orient themselves using Earth’s magnetic field.

Section 51.6: The Evolution of Self-Sacrificing Behavior

> **Altruism** is behavior that has a fitness cost to the individual exhibiting it and a fitness benefit to the recipient of the behavior.

> Altruism decreases an individual’s ability to produce offspring but helps others produce more offspring.
> The existence of altruistic behavior appears to be paradoxical, because if certain alleles make an individual more likely to be altruistic, those alleles should be selected against.

Kin Selection

> **Hamilton's rule** shows that individuals can pass their alleles on to the next generation not only by having their own offspring, but also by helping close relatives produce more offspring.
> **Hamilton’s rule** states that if the benefits of altruistic behavior are high, the benefits are dispersed to close relatives, and the costs are low, alleles associated with altruistic behavior will be favored by natural selection and will be spread throughout the population.
> This rule can be expressed as $Br > C$, where B is the fitness benefit to the beneficiary, r is the **coefficient of relatedness**, and C is the fitness cost to the actor.
> **Kin selection** is natural selection that acts through benefits to relatives.

Reciprocal Altruism

> **Reciprocal altruism** is an exchange of fitness benefits that are separated in time.
> Experimental evidence has shown that individual vervet monkeys are most likely to groom unrelated individuals that have groomed or helped them in the past, and vampire bats are most likely to donate blood meals to non–kin that have previously shared food with them.

Chapter 52: Population Ecology

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Key Concepts

> Life tables summarize how likely it is that individuals of each age class in a population will survive and reproduce.
> The growth rate of a population can be calculated from life-table data or from the direct observation of changes in population size over time.
> Researchers observe a wide variety of patterns when they track changes in population size over time, ranging from no growth, to regular cycles, to continued growth independent of population size.
> Data from population ecology studies help biologists evaluate prospects for endangered species and design effective management strategies.

Section 52.1 Outline: Demography

> **Demography** is the study of factors such as birth rates, death rates, and immigration and emigration rates, which determine the size and structure of populations through time.
> **Immigration** occurs when individuals enter a population by moving from another population.
> **Emigration** occurs when individuals leave a population to join another population.
> To predict the future of a population, biologists need to understand its makeup. If a population consists primarily of young individuals, the population size should increase; if it is made up chiefly of old individuals, the population size should decline.
> Biologists also need to know how many individuals of different ages immigrate and emigrate each **generation**—the average time between a mother's first offspring and her daughter's first offspring.

Life Tables

> A **life table** summarizes the probability that an individual will survive and reproduce in any given year over its entire lifetime.

Survivorship

> **Survivorship** is the proportion of offspring produced that survive, on average, to a particular age.
> A **survivorship curve** is a plot of the logarithm of the number of survivors versus age. Three general types of survivorship curves:
–In a type I curve, survivorship throughout life is high, and most individuals approach the maximum life span of the species.

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–In a type II curve, most individuals experience relatively constant survivorship over their lifetimes.

–Type III curves result from high death rates early in life, with high survivorship after maturity.

> Survivorship curves are important in conservation work because they pinpoint the stage of life when endangered species have particularly low survivorship.

Fecundity

> **Fecundity** is the number of female offspring produced by each female in the population.

> **Age–specific fecundity** is the average number of female offspring produced by a female in a given **age class**—a group of individuals of a specific age.

> **Fitness trade–offs** occur because every individual has a restricted amount of time and energy at its disposal– its resources are limited.

> An organism's **life history** consists of how the organism allocates resources to growth, reproduction, and activities related to survival.

> Life history trade–offs are universal.

> Life–history traits form a continuum.

> Within populations, life–history traits can change if conditions change. Such changes might directly affect a population's growth rate.

Section 52.2: Population Growth

> A population's growth rate is the change in the number of individuals in the population (ΔN) per unit time (Δt).

> If no immigration or emigration is occurring, the **per–capita rate of increase** (r) is the difference between the birth rate per individual (b) and the death rate per individual (d).

> If the per–capita birth rate is greater than the per–capita death rate, then r is positive and the population is growing.

> If the per–capita death rate begins to exceed the per–capita birth rate, then r is negative and the population declines.

> Within populations, r varies through time and can be positive, negative, or zero.

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> When birth rates per individual are as high as possible and death rates per individual are as low as possible, r reaches a maximum value called the **intrinsic rate of increase**, r_{max}.

> The population's growth rate is expressed as:

$\Delta N/\Delta t = r_{max}N$

> A species with a certain life history has a characteristic r_{max} that does not

change.
> The instantaneous growth rate of a population at a particular time is likely to be much lower than r_{max}.
> A population's r is also likely to be different from r values of other populations and to change over time.

Exponential Growth

> **Exponential growth** occurs when r does not change over time. It does not depend on the number of individuals in the population. When increases in the size of a population do not affect r, growth is **density independent**.
> When **population density**—the number of individuals per unit area—gets very high, we would expect the population's per–capita birth rate to decrease and the per–capita death rate to increase, causing r to decline. This type of growth is **density dependent**.

Logistic Growth

> **Carrying capacity**, K, is the maximum number of individuals in a population that can be supported in a particular habitat over a sustained period of time.
> If a population of size N is below the carrying capacity K, the population should continue to grow. Specifically, a population's growth rate should be proportional to (K – N)/K:

$\Delta N \Delta t = r_{max} N(K - N)/K$

> This expression is called the **logistic growth equation** and describes **logistic population growth**—a change in growth rate that occurs as a function of population size.

What Limits Growth Rates and Population Sizes?

> Population sizes change as a result of density–independent and density–dependent factors.

> **Density–independent factors** are usually abiotic (for example, variation in weather patterns) and change birth rates and death rates irrespective of the size of a population.
> **Density–dependent factors** are usually biotic (for example, an increase in predation rates on deer when population sizes are high) and change in intensity as a function of population size.
> Density–dependent effects on survivorship and fecundity cause logistic population growth.
> Carrying capacity varies among species and populations and this variation affects both growth rates and population sizes.
> Carrying capacity varies in space and time, and the same region may also have different carrying capacities for different species.

Section 52.3: Population Dynamics

> **Population dynamics** are the changes in populations through time.

> Results of a long–term study (begun in 1856) to examine the population dynamics of plants in a hay meadow showed distinct patterns of change in the populations of meadow species.

> In several cases, patterns of change over time appeared to correlate with life–history traits.

How Do Metapopulations Change through Time?

> If individuals from a species occupy many small patches of habitat so that they form many independent populations, they represent **metapopulations –** a population of populations.

> Within metapopulations, the overall population size stays relatively stable even if subpopulations go extinct (Figure 52.10b).

Why Do Some Populations Cycle?

> Some populations exhibit **population cycles**—regular fluctuations in size.

> Most hypotheses put forward to explain population cycles depend on some density–dependent factor. Predation, disease, or food shortages intensify dramatically at high population density and cause population numbers to crash.

How Does Age Structure Affect Population Growth?

> A population's **age structure**—the proportion of individuals that are at each possible age—has a dramatic influence on the population's growth over time.

Age Structure in a Woodland Herb

> The common primrose has a complex population dynamic.

> Populations dominated by juveniles experience rapid growth, then decline by a density–independent factor: the shading of larger trees.

> The long–term trajectory of the primrose population in an area may depend on the frequency and severity of windstorms that knock down trees and create sunlit gaps. If so, the dynamics of populations are governed by an abiotic, density–independent factor.

> Primroses form a metapopulation, a large number of subpopulations that will arise, grow, and go extinct over time.

Age Structure in Human Populations

> The age structures of human populations in different countries vary dramatically and can be represented by **age pyramids**—graphs with horizontal bars representing the numbers of males and females of each age group.

> The age distribution of a population tends to be uniform in more developed countries and bottom–heavy in less–developed countries.

> This bottom–heavy type of age distribution occurs when populations have undergone rapid growth and are dominated by the very young.

Analyzing Change in the Growth Rate of Human Populations

> The growth rate for humans has increased over the past 250 years, leading to a very steeply rising curve over the past few decades.
> Since 1970, however, the growth rate in human populations has been dropping. Between 1990 and 1995, the worldwide growth rate in human populations averaged 1.46% per year; currently the rate is 1.2% annually.

Will Human Population Size Peak in Your Lifetime?

> Figure 52.16 shows extrapolations of the world's population to the year 2050 based on three different fertility rates.
> When fertility at the **replacement rate** is sustained for a generation—each woman producing exactly enough offspring to replace herself and her offspring's father—**zero population growth** (**ZPG**) results.

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> The future of the human population hinges on fertility rates, on how many children each woman living today decides to have.

Section 52.4: How Can Population Ecology Help Endangered Species?

> Conservationists draw heavily on concepts and techniques from population ecology when designing programs to save species threatened with extinction.

Preserving Metapopulations

> An increasing number of species are being forced into a metapopulation structure.
> Over time, each population within a larger metapopulation is unlikely to survive over the long term.
> Important conservation messages:

– Areas that are being protected for threatened species should be substantial enough in area to maintain large populations that are unlikely to go extinct in the near future.

– When it is not possible to preserve large tracts of land, an alternative is to establish systems of smaller tracts that are connected by corridors of habitat, so that migration between patches is possible.

– If the species that is threatened exists as a metapopulation, it is crucial to preserve at least some patches of unoccupied habitat to provide future homes for immigrants. If a population is lost from a preserve, the habitat should continue to be protected so it can be colonized in the future.

Using Life–Table Data to Make Population Projections

> Life–table data can be used to project the future of a population.
> A population projection based on life tables allows the values for survivorship and fecundity to be altered at particular ages and the consequences to be assessed.

Population Viability Analysis

> A **population viability analysis** (**PVA**) is a model that estimates the likelihood that a population will avoid extinction for a given time period.
> A PVA attempts to combine basic demographic models with data on geographic structure and the rate and severity of habitat disturbance.

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> A PVA makes many assumptions about future events and is only as accurate as the data entered into it.

Chapter 53: Community Ecology

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Key Concepts

> Interactions among species, such as competition and consumption, have two main outcomes: (1) They affect the distribution and abundance of the interacting species, and (2) they are agents of natural selection and thus affect the evolution of the interacting species. The nature of interactions between species frequently changes over time.
> The assemblage of species found in a biological community changes over time and is primarily a function of climate and chance historical events.
> Species diversity is high in the tropics and lower toward the poles. The mechanism responsible for this pattern is still being investigated.

Section 53.1: Species Interactions

> Because the species in a community interact almost constantly, the fate of a particular population may be tightly linked to the other species that share its habitat.
> Biologists consider the effects of interactions among species on the fitness of the individuals involved.
> A relationship between two species that provides a fitness benefit to members of one species is a + interaction.
> Such a relationship that hurts members of the other species is a – interaction.
> A relationship that has no effect on the members of either species is a 0 interaction.
> **Commensalism** is a +/0 relationship.
> Species interactions may affect the distribution and abundance of a particular species.
> Species act as agents of natural selection when they interact. In biology, a **coevolutionary arms race** occurs between predators and prey, between parasites and hosts, and between other types of interacting species.
> The outcome of interactions among species is dynamic and conditional.

Competition

> **Competition** is a −/− interaction that occurs when individuals use the same limited resources.

- **Intraspecific competition** occurs between members of the same species.

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- Because intraspecific competition for resources intensifies as a population's density increases, it is a major cause of density–dependent growth.
- **Interspecific competition** occurs when members of different species use the same limiting resources.
- There are several mechanisms of interspecific competition:
  - –Consumptive competition occurs when two species consume the same resources.
  - –Preemptive competition exists when one species makes space unavailable to other species.
  - –Overgrowth competition happens when one species grows above another.
  - –Chemical competition takes place when one species produces toxins that negatively affect another species.
  - –Territorial competition arises when a mobile species protects its feeding or breeding territory against other species.
  - –Encounter competition occurs where two species interfere directly for access to specific resources.

Using the Niche Concept to Analyze Competition

- A **niche** can be thought of as the range of resources that the species is able to use or the range of conditions it can tolerate.
- Interspecies competition occurs when the niches of two species overlap.

What Happens When One Species Is a Better Competitor?

- The **competitive exclusion principle** states that it is not possible for species within the same niche to coexist.
- **Asymmetric competition** occurs when one species suffers a much greater fitness decline than the other.
- In **symmetric competition,** each species experiences a roughly equal decrease in fitness.
- If asymmetric competition occurs and the two species have completely overlapping niches, the stronger competitor is likely to dive the weaker competitor to extinction.
- There is an important distinction between a species' **fundamental niche**—the resources used or conditions tolerated in the absence of competitors—and its **realized niche**—the resources used or conditions tolerated when competition does occur.

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Experimental Studies of Competition

- Experimental evidence supports competitive exclusion of Chthamualus barnacles from the lower intertidal zone by Balanus barnacles.

Mechanisms of Coexistence: Fitness Trade–offs and Niche Differentiation

- The ability to compete for a particular resource is only one aspect of an organism's niche.
- If individuals are extremely good at competing for a particular resource, they are probably less good at enduring drought conditions, warding off disease, or preventing predation – there is a fitness trade–off.
- Because competition is a –/– interaction, there is strong natural selection on both species to avoid it.
- An evolutionary change in traits reduces the amount of niche overlap and the amount of competition.
- This change in resource use is called **niche differentiation** or resource partitioning. The change in species' traits is called **character displacement**.

Consumption

- **Consumption** occurs when on organism eats another.
- There are three major types of consumption:
- **Herbivory** is the consumption of plant tissues by **herbivores**.
- **Parasitism** is the consumption of small amounts of tissues from another organism, or **host**, by a **parasite**.
- **Predation** is the killing and consumption of most or all of another individual (the **prey**) by a **predator**.

How Do Prey Defend Themselves?

- **Standing** or **constitutive defenses** are defenses that are always present.
- **Mimicry** is the close resemblance of one species for another.
- **Müllerian mimicry** is the resemblance of two harmful prey species.
- **Batesian mimicry** is the resemblance of an innocuous prey species to a dangerous prey species.
- Prey have adaptations that reduce their likelihood of becoming victims. These adaptations are responses to natural selection exerted by predators.

- **Inducible defenses** are defenses produced only when prey are threatened.
- A study of the thickness of mussel shells demonstrated that thicker shells are an inducible defense produced by the presence of crabs.

Are Animal Predators Efficient Enough to Reduce Prey Populations?

- Species interactions have a strong impact on the evolution of predator and prey populations.
- Why Don't Herbivores Eat Everything – Why Is the World Green?

> A **meta–analysis**—a study of studies—of more than 100 studies raised the question of why herbivores don't eat more of the available plant food.
> Three hypotheses, all of which are correct, have been proposed to answer this question:
> The **top–down control hypothesis** states that predation or disease limits herbivores.
> The **poor–nutrition hypothesis** states that plants are a poor food source in terms of the nutrients they provide for herbivores and limits herbivore density.
> The **plant–defense hypothesis** states that plants defend themselves effectively enough to limit herbivory.

Adaptation and Arms Races

> A coevolutionary arms race between parasites and hosts begins when a parasitic species develops a trait that allows it to survive and reproduce in a host. In response, natural selection favors host individuals that are able to defend themselves against the parasite.
> An example is the interaction between the human immune system and Plasmodium.

Can Parasites Manipulate Their Hosts?

> Extensive coevolution occurs among species that interact via consumption.
> Snails infected with flukes become attracted to light and are therefore more easily eaten by birds, thus continuing the life cycle of the fluke.

Mutualisms

> **Mutualisms** are +/+ interactions that involve a wide variety of organisms and rewards.
> Even though mutualisms benefit both species, the interaction does not involve individuals from different species being altruistic.

> The benefits received in a mutualism are a by–product of each individual pursuing its own self–interest by maximizing its ability to survive and reproduce.
> Mutualism is like parasitism, competition, and other types of species interactions in that the outcome of the interaction depends on current conditions.
> Because the costs and benefits of species interactions are fluid, an interaction between the same two species may vary from parasitism to mutualism to competition.
> Table 53.1 summarizes the fitness effects, short–term impacts on population size, and long–term evolutionary aspects of species interactions.

Section 53.2: Community Structure

> Research on species interactions usually focuses on just two species at a

time, but biological communities contain many thousands of species. To understand how communities work, biologists explore how combinations of many species interact.

How Predictable Are Communities?

> Frederick Clements promoted the view that biological communities are stable, integrated, and orderly entities with a highly predictable composition.

> Clements argued that communities develop by passing through a series of predictable stages dictated by extensive interactions among species and that this development culminates in a stable final stage called a **climax community.**

> Henry Gleason contended that the community found in a particular area is neither stable nor predictable.

> According to Gleason, it is largely a matter of chance whether a similar community develops in the same area after a disturbance occurs.

Mapping Current and Past Species' Distributions

> If communities are predictable assemblages, the same group of species should almost always be found growing together.

> Historical data on plant communities showed that groups of species did not change their distributions in close association. Instead, species tended to change their ranges independently of one another.

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Experimental Tests

> A study of planktonic communities in ponds showed that identical communities do not develop in identical habitats after disturbance suggesting that Clements's position was too extreme and Gleason's view is closer to correct.

How Do Keystone Species Structure Communities?

> Even though species are not predictable assemblages, the structure of a community can change dramatically if a single species of predator or herbivore is removed from a community or added to it.

> A **keystone species** is a species that has a much greater impact on the surrounding species than its abundance would suggest.

Section 53.3: Community Dynamics

> Communities change through time and are dynamic.

Disturbance and Change in Ecological Communities

> Community composition and structure may change radically in response to changes in abiotic and biotic conditions.

> A **disturbance** is any event that removes some individuals or biomass from a community.

> The important feature of a disturbance is that it alters some aspect of resource availability.

> The impact of disturbance is a function of three factors:

–the type of disturbance
–its frequency
–its severity

> Most communities experience a characteristic type of disturbance, and in most cases, disturbances occur with a predictable frequency and severity.

> This is called a community's **disturbance regime**.

How Do Researchers Determine a Community's Disturbance Regime?

> Ecologists use two approaches to determine the pattern of disturbance in a community: (1) inference of long–term patterns from data obtained in short–term analysis, and (2) reconstruction of the history of a particular site.

Why Is It Important to Understand Disturbance Regimes?

> The results of a study to determine the history of disturbance in a fire–prone community from tree rings.

> This study established that fires are extremely frequent in the community examined.

> Biologists are now better able to manage these forests by allowing, monitoring, and controlling burns in them.

Succession: The Development of Communities after Disturbance

> **Succession** is the recovery that follows a severe disturbance.

> **Primary succession** occurs when a disturbance removes the soil and its organisms as well as organisms that live above the surface.

> **Secondary succession** occurs when a disturbance removes some or all of the organisms from an area but leaves the soil intact.

> The specific sequence of species that appears over time is the **successional pathway**.

Theoretical Considerations

> Biologists focus on three factors to predict the outcome of succession in a community: (1) the particular traits of the species involved; (2) how species interact; and (3) historical and environmental circumstances.

> **Pioneering species**—the first organisms to arrive at a newly disturbed site—have good dispersal ability and weedy histories.

> A **weed** is a plant that is adapted for growth in disturbed soils.

> Once colonization is under way, the course of succession tends to depend less on how species cope with aspects of the abiotic environment and more on how they interact with other species.

> During succession, existing species can have one of three effects on subsequent species: facilitation, tolerance, or inhibition.

> **Facilitation** takes place when the presence of an early–arriving species makes conditions more favorable for the arrival of certain later species by providing shade or nutrients.

> **Tolerance** means that existing species do not affect the probability that

subsequent species will become established.

> **Inhibition** occurs when the presence of one species inhibits the establishment of another.

> In addition to species traits and species interactions, the pattern and rate of succession depend on the historical and environmental context in which they occur.

A Case History: Glacier Bay, Alaska

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> An extraordinarily rapid and extensive glacial recession is occurring at Glacier Bay, and it has thus become an important site for studying succession.

> Three successional pathways have occurred.

> Successional pathways are determined by an array of factors, including the adaptations that certain species have to their abiotic environment, interactions among species, and the history of the site.

> Species traits and species interactions tend to make succession predictable, whereas history and chance events contribute a degree of unpredictability.

Section 53.4: Species Richness in Ecological Communities

> **Species richness** is the number of species present in a given community.

> **Species diversity** is a weighted measure that incorporates a species' relative abundance as well as its presence or absence.

Predicting Species Richness: The Theory of Island Biogeography

> Although larger patches of habitat generally contain more species than do smaller patches, islands in the ocean have smaller numbers of species than do areas of the same size on continents.

> Species richness varies as a function of island characteristics: the number of existing species, the island size, and the remoteness of the island.

> This model is called the theory of island biogeography.

Global Patterns in Species Richness

> Communities in the tropics have more species than communities in temperate or subarctic environments.

> As latitude increases, species diversity decreases.

> Several key hypotheses explain this pattern:

> The high–productivity hypothesis proposes that high productivity promotes high diversity.

> The energy hypothesis contends that high temperature increases productivity and the likelihood that organisms can tolerate the physical conditions in a region.

> A third hypothesis argues that the tropical regions have had more time for speciation than other regions.

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> The **intermediate disturbance hypothesis** states that regions with a moderate type, frequency, and severity of disturbance should have high species richness and diversity.

> Each of these factors may influence diversity, but no single hypothesis offers a convincing explanation for the global diversity gradient.

Chapter 54: Ecosystems

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Key Concepts

> An ecosystem has four components: (1) the abiotic environment, (2) primary producers, (3) consumers, and (4) decomposers. These components are linked by the movement of energy and nutrients.

> The productivity of terrestrial ecosystems is limited by warmth and moisture, while nutrient availability is the key constraint in aquatic ecosystems. As energy flows from producers to consumers and decomposers, much of it is lost.

> To analyze nutrient cycles, biologists focus on the nature of the reservoirs where elements reside and on how quickly elements move between reservoirs.

> Humans are causing large, global changes in the abiotic environment. The burning of fossil fuels has led to rapid global warming. Extensive fertilization is increasing productivity and causing pollution.

Section 54.1: Energy Flow and Trophic Structure

> Ecosystems have four components: the abiotic environment, primary producers, consumers, and decomposers. These components are linked by a flow of energy.

> A **primary producer**, or **autotroph**, is an organism that can synthesize its own food from inorganic sources.

> Primary producers form the basis of ecosystems by transforming the energy in sunlight or inorganic compounds into the chemical energy stored in sugars.

> They use this chemical energy for maintenance, respiration, growth, and reproduction.

> The energy invested in new tissue is called **net primary productivity** (**NPP**).

> NPP represents the amount of energy available to **consumers**—organisms that eat other organisms.

> **Herbivores** eat plants; **carnivores** eat animals.

> **Decomposers**, or detritivores, feed on waste products or the dead remains of other organisms.

> The **abiotic environment** includes the soil, the climate, the atmosphere, and the particulate matter and solutes in water.

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> Energy moves from the Sun or inorganic compounds to consumers, decomposers, and the abiotic environment.

Global Patterns in Productivity

> NPP varies among ecosystems by region and by biome.

What Limits Productivity?

> Overall productivity of terrestrial ecosystems is limited by a combination of temperature and the availability of water and sunlight.

> The overall productivity of marine ecosystems is limited by the availability of nutrients.

How Does Energy Flow through an Ecosystem?

> Net primary productivity results in **biomass**, organic material that non–photosynthetic organisms can eat.

> In all environments, the chemical energy in primary producers eventually moves to one of two types of organisms: primary consumers or primary decomposers.

> The **primary consumer** is an herbivore that eats plants or algae or other photosynthetic cells.

> **Detritus**, dead animals and dead plant tissues, is consumed by **primary decomposers.**

Trophic Levels, Food Chains, and Food Webs

> **Trophic levels** identify steps in energy transfer, and organisms that obtain their energy from the same type of source occupy the same trophic level.

> A **food chain** connects the trophic levels in a particular ecosystem.

> The **grazing food chain** is composed of the network of herbivores (primary consumers) and the organisms that eat herbivores (secondary consumers).

> The **decomposer food chain** is made up of species that eat the dead remains of organisms.

> Food chains are usually embedded in more complex **food webs.**

> Food webs are a more complete description of the trophic relationships among the organisms in an ecosystem (Figure 54.6).

Why Is Energy Lost at Each Trophic Level?

> All ecosystems exhibit a pattern—the **pyramid of productivity**—in which productivity is greatest at the lowest trophic level and declines at higher levels.

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> This pattern occurs because some energy is necessarily lost in keeping an organism alive—such as the heat required for metabolism and the energy a predator needs to capture prey—at each trophic level.

What Limits the Length of Food Chains?
> Food chains and food webs have only two to seven trophic levels.
> Three hypotheses have been advanced to explain this observation
> The energy–transfer hypothesis proposes that food–chain length is limited by productivity.
> Because a large fraction of the energy transferred up a food chain is lost, there may not be enough left to support an additional suite of consumers by the time energy reaches the top trophic level.
> The stability hypothesis suggests that long food chains are easily disrupted by environmental perturbations and thus tend to be eliminated.
> The environmental–complexity hypothesis argues that food–chain length is a function of an ecosystem's physical structure.
> Three–dimensional ecosystems should have longer food chains than do two–dimensional ecosystems.
> Research to date shows that there is unlikely to be a single simple answer to the question of what limits food–chain length.
> Inefficiencies of energy transfer, environmental stability, and environmental complexity may all influence the number of trophic levels that can be supported in a given ecosystem.

Analyzing Energy Flow: A Case History
> The Hubbard Brook Forest is a model ecosystem for studying energy and nutrient flow.
> For this ecosystem, researchers calculated the **gross primary productivity** —the total amount of photosynthesis in a given area and time period—and the **gross photosynthetic efficiency**—the efficiency with which plants use the total amount of energy available to them.
> **How Does Energy Flow through the Hubbard Brook Ecosystem?**
> Results showed that only a small fraction of the energy consumed by a primary consumer is used for **secondary production**, the production of new tissue by primary consumers.
> Most of the energy is used for maintenance.
> The general pattern for the Hubbard Brook ecosystem is typical of ecosystems around the globe.

Section 54.2: Biogeochemical Cycles
> A **biogeochemical cycle** is the path that an element takes as it moves from abiotic systems through living organisms and back again.
> To get a basic understanding of how a biogeochemical cycle works, researchers focus on three fundamental questions:
–What are the nature and size of the **reservoirs**, or areas where elements are stored for a period of time?
–How fast does the element move between reservoirs, and what

factors influence these rates?

–How does any given biogeochemical cycle interact with other cycles?

Biogeochemical Cycles in Ecosystems

- Nutrients cycle from organism to organism in an ecosystem via assimilation, consumption, and decomposition. Nutrients are exported from ecosystems when water or organisms leave the area (Figure 54.10).

What Functions Control the Rate of Nutrient Cycling in Ecosystems?

- Most often, decomposition of detritus limits the rate at which nutrients move through an ecosystem.
- Decomposition rate is influenced by abiotic conditions and the quality of the detritus as a nutrient source.

What Factors Influence the Rate of Nutrient Loss?

- A study was done on two **watersheds** (areas drained by a single stream)—one with all vegetation removed (the experimental treatment), the other left undisturbed (the control).
- This study showed that devegetation greatly increases nutrient export

Global Biogeochemical Cycles

- When nutrients leave one ecosystem, they enter another.
- The movement of ions and molecules among ecosystems links local biogeochemical cycles into one massive global system.

The Global Water Cycle

- Figure 54.13 shows a simplified version of the **global water cycle**.
- Water evaporates out of the ocean and precipitates back into it. For this component of the cycle, evaporation exceeds precipitation, resulting in a net gain of water to the atmosphere over the oceans.

- When this water vapor moves over the continents, it is augmented by small amounts of water that evaporates from lakes and streams and by large amounts of water transpired by plants. The total volume of water in the atmosphere over land is balanced by the amount of precipitation that occurs on the continents.
- The cycle is completed both by water that moves from the land to the oceans via streams and by **groundwater**—water that is found in soil.

The Global Carbon Cycle

- The **global carbon cycle** involves the movement of carbon among terrestrial ecosystems, the oceans, and the atmosphere.
- The ocean is by far the largest of these three reservoirs. Carbon moves into and out of the atmospheric reservoir rapidly via the photosynthesis and respiration of organisms.
- Carbon dioxide is a **greenhouse gas**—gas that traps heat radiated from Earth and keeps it from being lost to space.
- Increases in the amounts of greenhouse gases have the potential to

warm Earth’s climate by increasing the atmosphere’s heat–trapping potential.

- Human activities such as intensive agriculture, deforestation, and the burning of fossil fuels have changed the carbon cycle by adding large amounts of carbon dioxide to the atmosphere.

The Global Nitrogen Cycle

- The vast majority of molecular nitrogen (N_2) in the atmosphere is unavailable to plants because they can use nitrogen only in the form of ammonium (NH_4^+) or nitrate (NO_3^-) ions.
- Nitrogen is added to ecosystems in a usable form only when it is reduced (or fixed)—converted from N_2 to NH_3. Nitrogen fixation results from lightning–driven reactions in the atmosphere and from enzyme–catalyzed reactions in bacteria that live in the soil and oceans.
- Human–fixed nitrogen in the form of fertilizers, nitric oxide from burning fossil fuels, and cultivation of certain crops is having a major impact on the nitrogen cycle.

Section 54.3: Human Impacts on Ecosystems

- Two factors are responsible for the human impacts on ecosystems: the rapid increase in human population and the rapid increase in human resource use.
- Residents of industrialized countries, though relatively few in number, have a disproportionately large impact on biogeochemical cycles because they use so much energy, water, food, and other resources.

Global Warming

- **Global warming** is an increase in Earth's surface temperature, averaged over the globe.
- Current evidence clearly shows that human activities have had an effect on global warming, mainly through an increase in greenhouse gases.
- The models currently being used suggest that average global temperature will undergo additional increases of up to 1.1–6.4ºC (2.0–11.5ºF) by the year 2100.
- Biologists have also documented the dramatic impacts of warming temperatures on organisms.

Productivity Changes

- Several of the changes that humans are inducing in biogeochemical cycles alter NPP.
- Increased productivity can be beneficial for certain ecosystems but can also have negative effects.
- Negative effects of increased productivity include a decline in species richness, anaerobic "dead zones," and harmful algal blooms.

Chapter 55: Biodiversity and Conservation

Key Concepts

> Biodiversity can be analyzed at the genetic, species, and ecosystem levels.

> If recent rates of extinction due to human population growth and habitat destruction continue, a mass extinction will occur.

> Humans depend on biodiversity for the products that wild species provide and for ecosystem services that protect the quality of the abiotic environment.

Section 55.1: What Is Biodiversity?

> The tree of life describes the evolutionary relationships among all forms of life. The branches represent all of the lineages of organisms living today and the tips represent all of the species.

> When biodiversity increases, branches and tips are added to the tree. When extinctions occur, tips and perhaps branches are removed.

Biodiversity Can Be Measured and Analyzed at Several Levels

> Biologists recognize and analyze biodiversity on three levels: genetic diversity, species diversity, and ecosystem diversity. Biodiversity is dynamic—it has been changing since life on Earth began.

> **Genetic diversity** is the total genetic information contained within all individuals of a species, measured as the number and relative frequency of all alleles present in a species.

> **Species diversity** is the variety of life–forms on Earth, measured as the number and relative frequency of species in a particular region.

> Taxonomic diversity encompasses the evolutionary relationships among the species present in a region. Some lineages on the tree of life are species–rich; others may be represented by only a single living species.

> **Ecosystem diversity** is the variety of biotic communities in a region, along with abiotic components such as soil, water, and nutrients.

> Attempts to measure ecosystem diversity focus on capturing the array of biotic communities and the variation of physical conditions in a region.

How Many Species Are Living Today?

> Approximately 1.5 million species have been cataloged to date, but represent only a tiny fraction of the number actually present.

> Two general approaches have been used to estimate the total number of species. One is based on intensive surveys of species–rich groups at small

sites and the other is based on attempts to identify all of the species present in a particular region.

Taxon–Specific Surveys

> Based on taxon–specific surveys, biologists estimate that at least 10

million and possibly as many as 100 million species of arthropods exist.
> **All–Taxa Surveys**
> The first effort to find and catalog all of the species present in a large area, the , is now under way.
> Over 650 new species have been discovered.

Section 55.2: Where Is Biodiversity Highest?
> In most taxomic groups, species richness is highest in the tropics and declines towards the poles. The tropical rainforests are particularly species rich.
> **Hotspots** are regions that are much more species rich than others.
> Conservation hotspots are regions that contain at least 1500 endemic plant species and for which at least 70 percent of their traditional or primary vegetation has been lost.
> These conservation hotspots are areas that are in most urgent need of conservation action and where efforts to preserve habitat would have the highest return on investment.

Section 55.3: Threats to Biodiversity
> Although extinction is natural, the rates of extinction are increasing.
> Modern rates of extinction are 100 to 1000 times greater than the average, or background, rate recorded in the fossil record over the past 550 million years.
> Directly or indirectly, recent extinctions are being caused by the demands of a rapidly growing human population.

Humans Have Affected Biodiversity throughout History
> Fossil evidence on islands in the South Pacific suggests that about 2000 bird species were wiped out as people colonized this area between about A.D. 1200.

Current Threats to Biodiversity
> Most extinctions that have occurred over the past 1000 years took place on islands as the result of overhunting or introduction of **exotic species**.

> **Endangered species**, species that are almost certain to go extinct without effective conservation programs, are now more likely to live on continents than on islands.
> Habitat destruction has replaced overhunting and species introduction as the primary threat to such species.
> Recent analysis of causes of endangerment for 488 endangered species native to Canada show several patterns (Figure 55.6):

–Virtually all of the endangered species are affected by more than one factor.

–Habitat loss is the single most important factor in the decline of these species.

–Overharvesting is the dominant problem for marine species while

pollution plays a large role for freshwater species.
–Factors beyond human control can also be important.

Habitat Destruction

> Humans cause **habitat destruction** in many ways, from logging and burning forests to grazing livestock to filling in wetlands and building housing developments.

> **Habitat Fragmentation**

> Human activities also result in **habitat fragmentation**—the breakup of large, contiguous areas of natural habitat into small, isolated pieces.

> Habitat fragmentation can reduce habitats to a size that is too small to support some species.

> Fragmentation also reduces the ability of individuals to disperse from one habitat to another, and may force species into metapopulations. This can lead to inbreeding depression and random loss of alleles due to genetic drift.

> When habitats are fragmented, the quality and quantity of habitat decline drastically.

How Can Biologists Predict Future Extinction Rates?

> Biologists use direct counts and species–area relationships to estimate current extinction rates and product how they might change in the near furure.

Estimates Based on Direct Counts

> The best information on current extinction rates comes from studies on birds.

> Recent analyses suggest that birds have been going extinct at a rate 100 times the background rate, or at a rate of one species per year rather than one species per 100 years. This rate is expected to increase.

Species–Area Relationships

> Species–area curves are used to analyze the relationship between species richness and habitat area.

> Over many different habitat types, the relationship is consistently described by the function S = cAz, where S is the number of species, c is a constant that is high in species–rich areas and low in species–poor areas, A is habitat area, and z is the slope of the line on a log–log plot of species number versus area.

Section 55.4: Preserving Biodiversity

> The conservation of biodiversity is urgent because, unlike other environmental problems, extinction is irreversible.

> The only solution to the biodiversity crisis is to prevent the loss of alleles, species, and ecosystems.

> In almost every case, the underlying causes of the biodiversity crisis are socioeconomic factors that encourage the short–term overexploitation of

land and other resources and discourage the long–term **sustainability** of resources.

> **Sustainability** is the managed use of resources at a rate only as fast as the rate at which they are replaced.

Why Is Biodiversity Important?

> The benefits of biodiversity extend beyond the direct use of diverse genes and species by humans to include ecosystem services – processes that increase the quality of the abiotic environment.

> Biodiversity affects human health and well–being both directly and indirectly. Direct benefits include goods and services provided by the environment. Indirect benefits include ways that biodiversity aids humans by contributing to a healthy overall environment.

Biodiversity Increases Productivity

> The experiment in Figure 55.14 demonstrates that the productivity of ecosystems depends on the number and type of species present, or the biodiversity.

> Biodiversity affects human health and well–being both directly and indirectly. Direct benefits include goods and services provided by the environment. Indirect benefits include ways that biodiversity aids humans by contributing to a healthy overall environment.

> Species richness has a positive impact on **net primary productivity** (NPP), the total amount of photosynthesis per unit area per year that ends up in biomass.

> This may be due to resource use efficiency, facilitation, and sampling effects.

Does Biodiversity Lead to Stability?

> The stability of a community refers to its ability to: (1) withstand a disturbance without changing, (2) recover to former levels of productivity or species richness after a disturbance, and (3) maintain productivity and other aspects of ecosystem function as conditions change over time.

> **Resistance** is a measure of how much a community is affected by a disturbance.

> **Resilience** is a measure of how quickly a community recovers following a disturbance.

> Diversity leads to high resistance and resilience (Figure 55.15).

> Increased biodiversity increases the services provided by ecosystems. It can then be inferred that if ecosystems are simplified by extinctions, then productivity and other attributes might decrease.

Designing Effective Protected Areas

> The **Gap Analysis Program (GAP)** identifies gaps between geographic areas that are particularly rich in biodiversity and areas that are actually managed for conservation.

- One recent GAP analysis combined data sets on the distribution of mammals, birds, amphibians, and freshwater turtles with a map of world protected areas. The analysis revealed that the ranges of many species occur completely outside any protected areas.
- Most GAP analyses suggest that the 11.5 percent of Earth's surface area that is now being managed for biodiversity will not be enough to conserve many species.
- Wildlife corridors that connect populations that would otherwise be isolated are being created.

- The goals of these corridors are to allow areas to be recolonized if a species is lost and introduce new alleles that would counteract the deleterious effects of genetic drift and inbreeding.
- Experimental evidence suggests that wildlife corridors work.