Chapter 54

Community Ecology

AP Biology

Overview: A Sense of Community

- This chapter will examine ecological interactions between populations of different species
  - A biological **community** is an assemblage of populations of various species living close enough for potential interaction
- We will discuss:
  - Types of interactions that occur between species in a community
  - Significant factors that structure communities
    - Dominant and keystone species
    - Disturbances
    - Biogeographic factors
  - Applications of community ecology to the study of human disease

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

- Ecologists call relationships between species in a community **interspecific interactions**
  - Examples include:
    - Competition
    - Predation
    - Herbivory
    - Symbiosis (including parasitism, mutualism, and commensalism)
- Interspecific interactions can affect the survival and reproduction of each species
  - Their effects on each species can be summarized as positive (+), negative (–), or no effect (0)

Competition

- **Interspecific competition** (–/– interaction) occurs when different species compete for a resource in short supply
  - Ex) Weeds growing in a garden compete with garden plants for soil nutrients and water
  - Ex) Lynx and foxes in the northern forests of Alaska and Canada compete for prey, including snowshoe hares

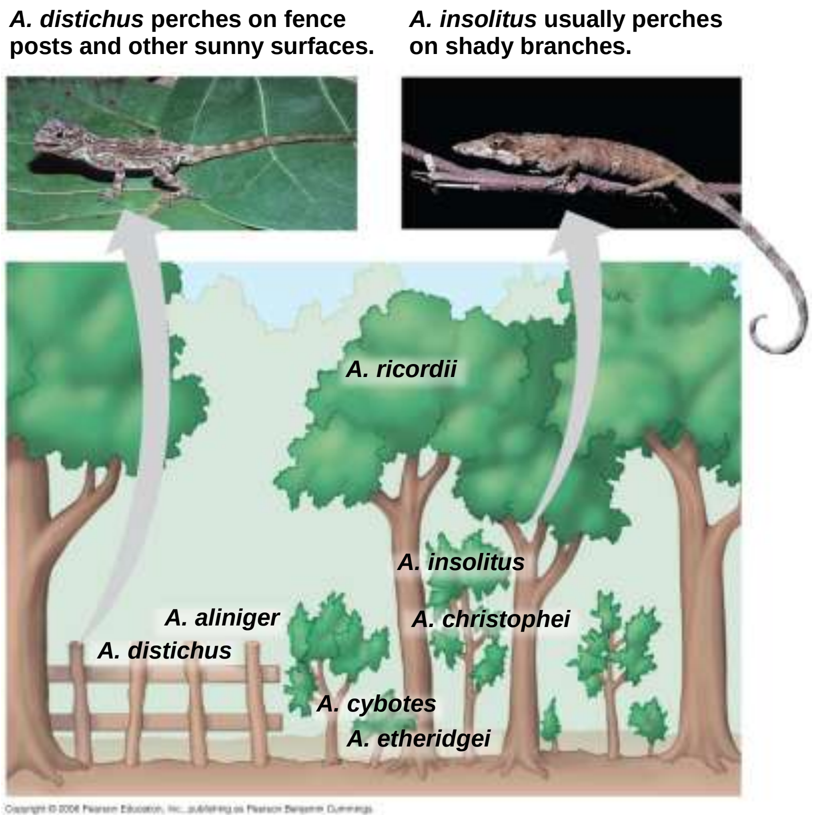
Competitive Exclusion

- Strong competition for a limited resource can lead to **competitive exclusion**, the local elimination of a competing species
  - The *competitive exclusion principle* states that two species competing for the same limiting resources cannot coexist in the same place
    - Even a slight reproductive advantage will eventually lead to local extinction of the inferior competitor
      - Ex) When ecologists grew 2 closely related species of protists in the same culture, with constant amounts of food provided daily, one of the species was eventually eliminated

Ecological Niches

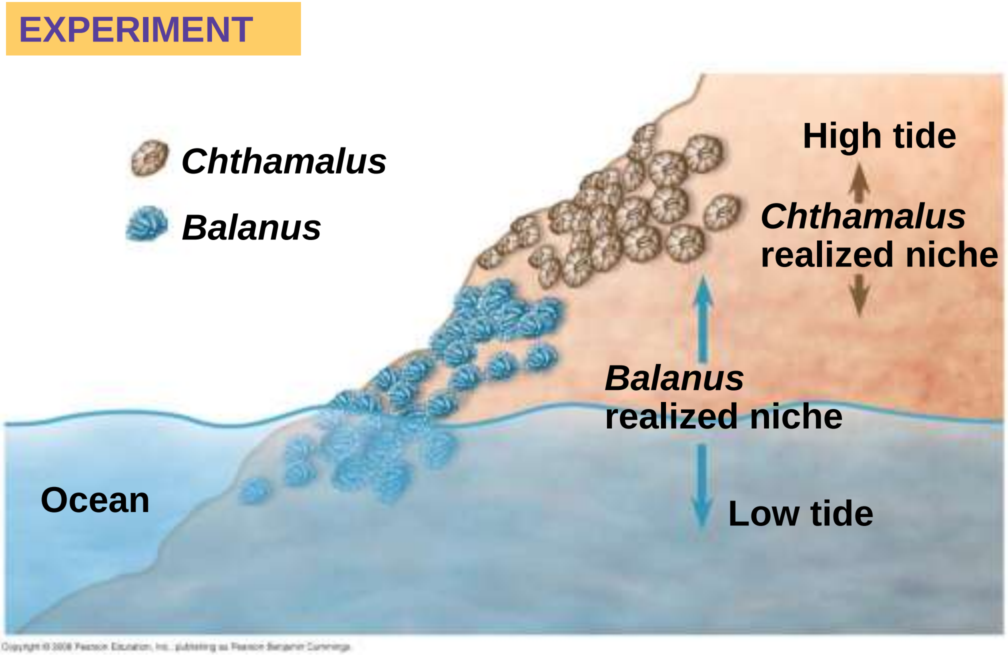
- The total of a species' use of biotic and abiotic resources is called the species' **ecological niche**
  - An ecological niche can also be thought of as an organism's ecological role (how it "fits into" an ecosystem)
    - Ex) The niche of a tropical tree lizard consists of many components, including
      - The temperature range it tolerates
      - The size of the branches on which it perches
      - The time of day it is active
      - The sizes and kinds of insects it eats

- The niche concept can be used to restate the principle of competitive exclusion:
  - Two species cannot coexist permanently in a community if their niches are identical
  - Ecologically similar species can coexist in a community only if there are one or more significant differences in their niches
- When competition between species with identical niches does not lead to local extinction of either species, it is usually because one species' niche become modified
  - One of the species thus begins to use a different set of resources
  - This differentiation of ecological niches that allows similar species to coexist in a community is called **resource partitioning**

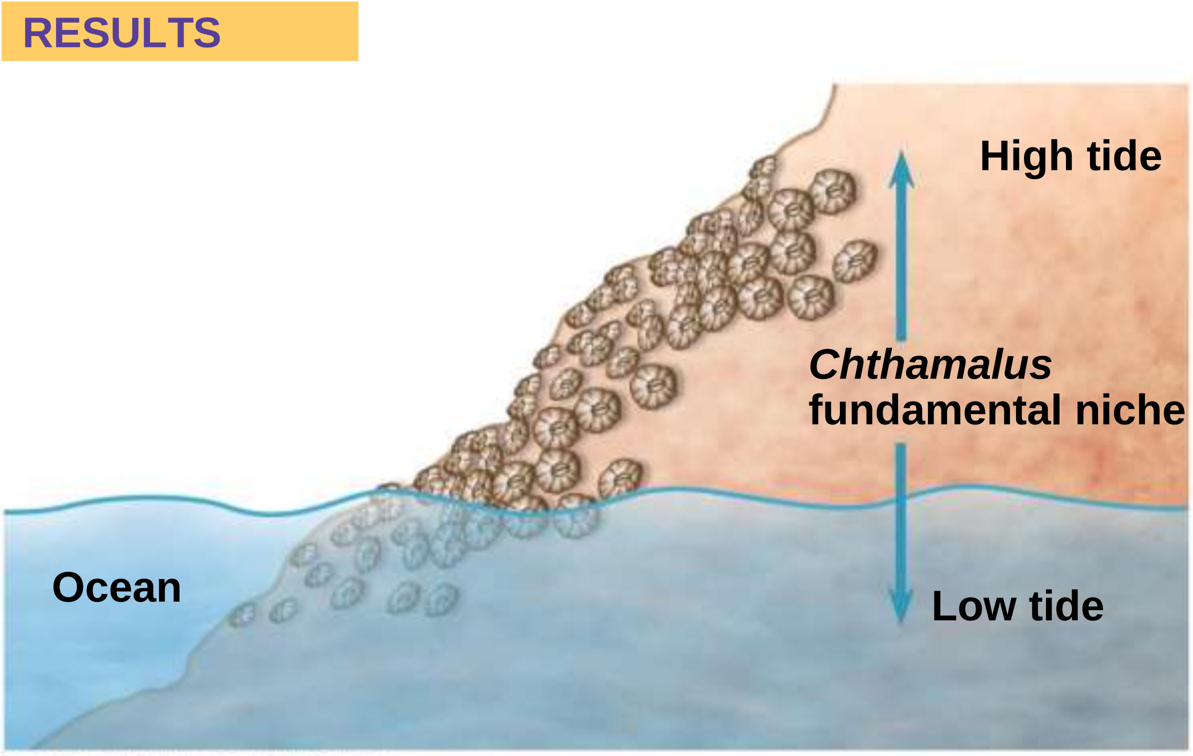


- As a result of competition, a species' fundamental niche may differ from its realized niche
  - *Fundamental niche*: the niche that can potentially be occupied by a species
  - *Realized niche*: the portion of a species' fundamental niche that it actually occupies in a specific environment
- Ecologists can identify the fundamental niche of a species by testing the range of conditions in which it can grow and reproduce in the absence of predators
  - They can also test whether a potential competitor limits a species' realized niche by removing the competitor and observing the results
    - Ex) Competition among barnacles

- **<u>Experiment</u>**:
  - Ecologists studied 2 barnacle species that have a stratified (layered) distribution on rocks along the coast of Scotland
    - *C. stellatus* is usually found higher on the rocks
    - *B. balanoides* is usually found lower on these same rocks
  - To determine whether the distribution of these species is the result of interspecific competition, ecologists removed *B. balanoides* from rocks at several sites



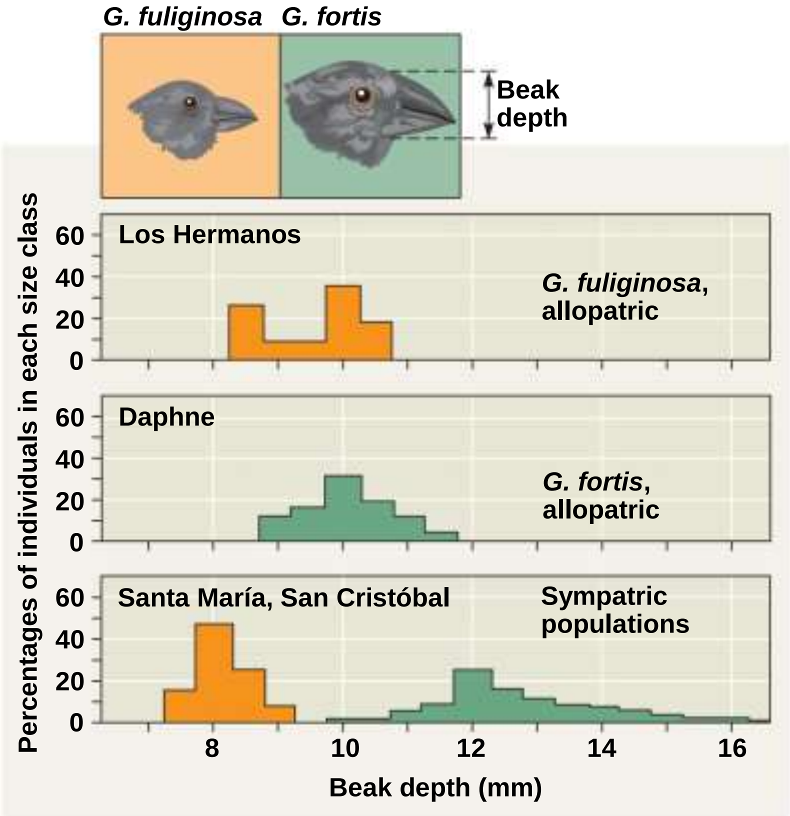
- **Results:**
  - *C. stellatus* spread into the region formerly occupied by *B. balanoides*
- **Conclusion:**
  - Interspecific competition makes the realized niche of *C. stellatus* much smaller than its fundamental niche



Character Displacement

- The geographic relationship between 2 closely related species also provides more evidence for the importance of competition in structuring communities
  - Allopatric (geographically separated) populations tend to be morphologically similar and use similar resources
  - Sympatric (geographically overlapping) populations, which must potentially compete for resources, tend to show differences in body structure and in the resources they use
    - This tendency for characteristics to be more divergent in sympatric populations of two species than in allopatric populations of the same two species is called **character displacement**
      - Ex) Variation in beak size between populations of two species of Galápagos finches

- Allopatric populations of *G. fuliginosa* and *G. fortis* on 2 different Galapagos Islands have similar beak morphologies (top 2 graphs)
  - They also presumably eat similarly-sized seeds
- Where these same 2 species are sympatric, however (bottom graph), *G. fuliginosa* has a shallower, smaller beak and *G. fortis* has a deeper larger one
  - These adaptations favor eating different sizes of seeds, thus reducing competition



Predation

- **Predation** (+/– interaction) refers to interaction where one species, the predator, kills and eats the other, the prey
  - Adaptations of predators and prey tend to be refined through natural selection
    - Some feeding adaptations of predators include:
      - Acute senses that allow them to locate and identify potential prey
        - Some organisms (ex: rattlesnakes) have a pair of heat-sensing organs between their eyes and nostrils to help locate prey
      - Claws, teeth, fangs, stingers, and poison that help predators catch and subdue their prey
      - Quickness and agility for those predators that must pursue their prey
      - Camouflage for those predators that lie and wait to ambush their prey

- Prey also display various defensive adaptations
  - Behavioral defenses include hiding, fleeing, forming herds or schools, self-defense, and alarm calls
    - Active self-defense is less common, though some large, grazing mammals vigorously defend their young from predators
  - Animals also have morphological and physiological defense adaptations
    - **Cryptic coloration**, or camouflage, makes prey difficult to spot

(a) Cryptic coloration

▶ Canyon tree frog

PLAY

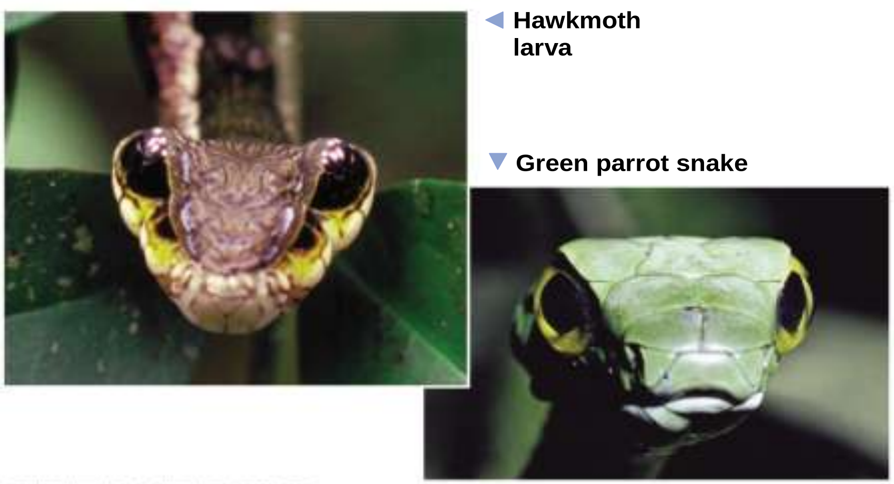
Video: Seahorse Camouflage

- Some animals also have mechanical or chemical defenses, including the skunk and porcupine
  - Animals with effective chemical defense (ex: poison dart frog) often exhibit bright warning coloration, called **aposematic coloration**
    - The fact that predators are particularly cautious in dealing with prey that display such coloration is evidence for this traits adaptive value

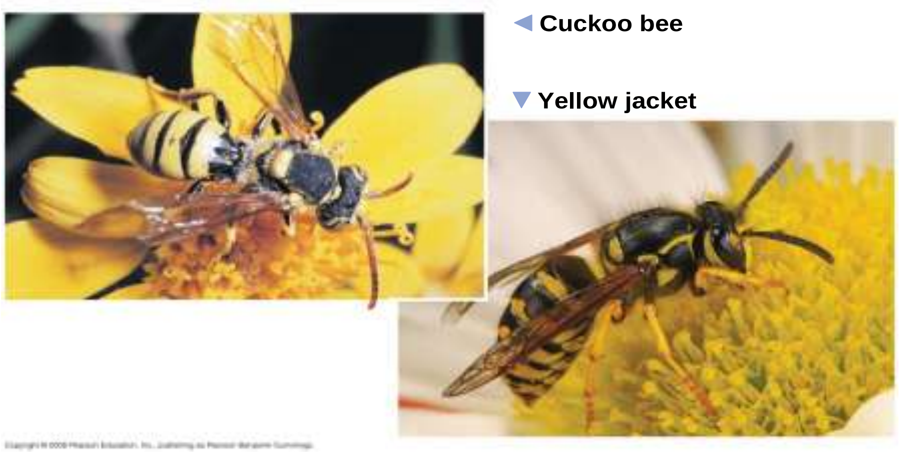
(b) Aposematic coloration

▶ **Poison dart frog**

- Other prey gain significant protection by mimicking the appearance of other species
  - In **Batesian mimicry**, a palatable or harmless species (hawkmoth larva) mimics an unpalatable or harmful model (green parrot snake)
  - In **Müllerian mimicry**, two or more unpalatable species (cuckoo bee and yellow jacket) resemble each other
    - Each species thus gains an additional advantage because, the more unpalatable prey there are, the more quickly and effectively predators adapt by avoiding any prey with that appearance



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



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

Herbivory

- **Herbivory** (+/– interaction) refers to an interaction in which an herbivore eats parts of a plant or alga
  - Like predators, herbivores have many specialized adaptations
    - Many herbivores (insects) have chemical sensors on their feet that allow them to distinguish between toxic and nontoxic plants, as well as between more nutritious and less nutritious plants
    - Some mammals (ex: goats) use their sense of smell to examine plants, rejecting some and eating others
    - Many herbivores also have specialized teeth or digestive systems adapted for processing vegetation

- Because plants cannot run away to avoid being eaten, their adaptations feature chemical or morphological defensive structures
  - Many plants contain chemical toxins that are poisonous or distasteful
    - Ex) Plants in the genus *Astragalus*, sometimes called “locoweeds” accumulate selenium toxins that cause cattle and sheep that eat them to wander aimlessly in circles or even die
  - Other plants have spines or thorns to discourage herbivores

Symbiosis

- **Symbiosis** is a relationship where two or more species live in direct and intimate contact with one another
  - This textbook adopts a general definition of symbiosis that includes all such interactions, whether harmful, helpful, or neutral, including:
    - Parasitism
    - Mutualism
    - Commensalism
  - Some biologists define symbiosis more narrowly as a synonym for mutualism, in which both species benefit

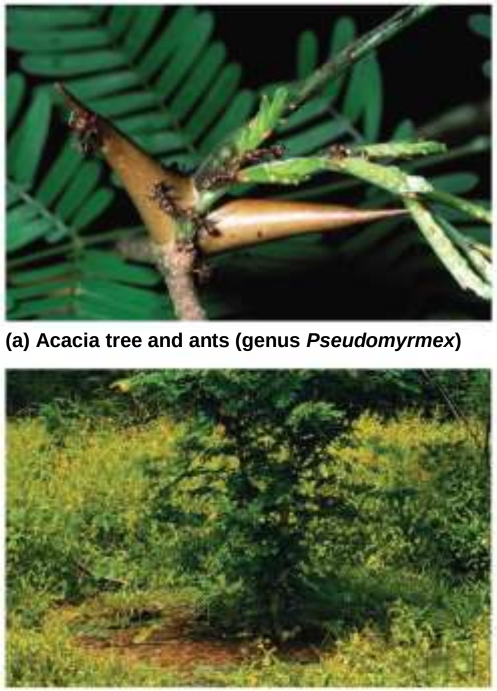
Parasitism

- In **parasitism** (+/– interaction), one organism, the **parasite**, derives nourishment from another organism, its **host**, which is harmed in the process
  - Parasites that live within the body of their host are called **endoparasites**
    - Ex) Tapeworms
  - Parasites that live on the external surface of a host are **ectoparasites**
    - Ex) Ticks and lice
  - Many parasites have complex life cycles involving multiple hosts
    - Ex) The life cycle of a blood fluke involves both humans and freshwater snails

- Some parasites change the behavior of their hosts in a way that increases the probability of the parasite being transferred from one host to another
  - Ex) Parasitic acanthocephalan worms cause their crustacean hosts to leave their protective cover and move out to open areas
    - Here, they have a greater chance of being eaten by birds, who are the second hosts in this worm's life cycle
- Parasites can significantly affect the survival, reproduction, and density of their host population
  - Ex) Ticks that live as ectoparasites on moose weaken their hosts by withdrawing blood and causing hair breakage and loss
    - This increases the chances that the moose will die from cold stress or predation by wolves

Mutualism

- Mutualistic symbiosis, or **mutualism** (+/+ interaction), is an interspecific interaction that benefits both species
  - A mutualism can be
    - *Obligate*, where one species cannot survive without the other
      - Ex) Termites and microorganisms in their digestive system that help them digest wood
    - *Facultative*, where both species can survive alone
      - Ex) Certain species of acacia trees in Central and South America have hollow thorns that house stinging ants
        - These ants feed on nectar produced by the tree and on protein-rich swellings at the tips of leaflets
        - The acacia benefits because the ants attack anything that touches the tree, remove fungal spores, small herbivores and debris, and clip vegetation that grows close to the tree



(a) Acacia tree and ants (genus *Pseudomyrmex*)

(b) Area cleared by ants at the base of an acacia tree

Commensalism

- In **commensalism** (+/0 interaction), one species benefits and the other is apparently unaffected
  - Commensal interactions are hard to document in nature because any close association usually affects both species
  - Some associations that are possibly commensal involve one species obtaining food that is inadvertently exposed by another
    - Ex) Cowbirds and cattle egrets feed on insects flushed out of grass by grazing bison, cattle, horses, and other herbivores
      - The birds thus benefit from this association, in that they increase their feeding success
      - Often, the herbivores may be unaffected by this relationship
        - However, these herbivores may also occasionally benefit when these birds happen to remove or eat ticks and other ectoparasites from them

Concept Check 54.1

- 1) Explain how interspecific competition, predation, and mutualism differ in their effects on the interacting populations of 2 species.
- 2) According to the principle of competitive exclusion, what outcome is expected when 2 species with identical niches compete for a resource? Why?
- 3) Suppose you live in an agricultural area. What examples of the 4 types of community interaction (competition, predation, herbivory, and symbiosis) might you see in the growing or use of food?

Concept 54.2:
Dominant and keystone species exert strong controls on community structure

- In general, some species in a community exert strong control on that community’s structure, including:
  - Community composition
  - Relative abundance of other species
  - Diversity of species
- Before examining the effects of these species, 2 fundamental features of community structure must be examined:
  - Species diversity
  - Feeding relationships

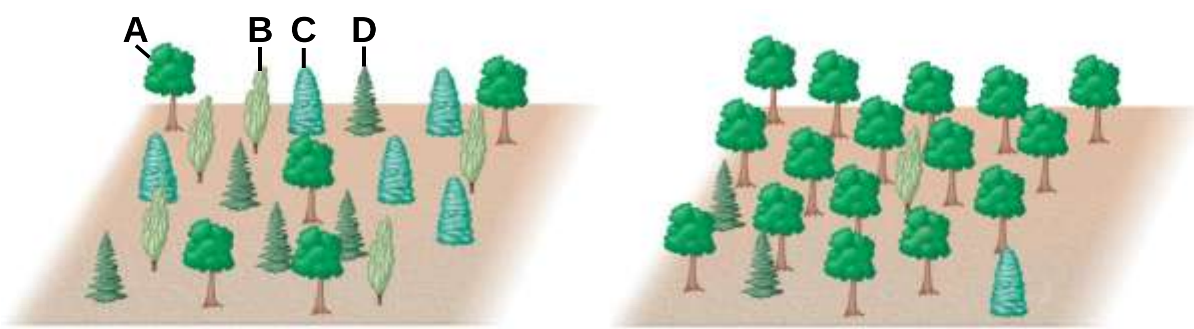
Species Diversity

- The **species diversity** of a community is the variety of organisms that make up the community
  - It has two components: species richness and relative abundance
    - **Species richness** is the total number of different species in the community
    - **Relative abundance** is the proportion each species represents of the total individuals in the community

- Ecologists use many tools to quantitatively compare the diversity of different communities
  - They often calculate the index of diversity based on species richness and relative abundance
  - One widely used index is the **Shannon diversity** (*H*)

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

    - A, B, C, ect. = species in the community
    - p = relative abundance of each species
  - Based on this index, which community below is more diverse?
    - Hint: A higher value for H indicates greater diversity

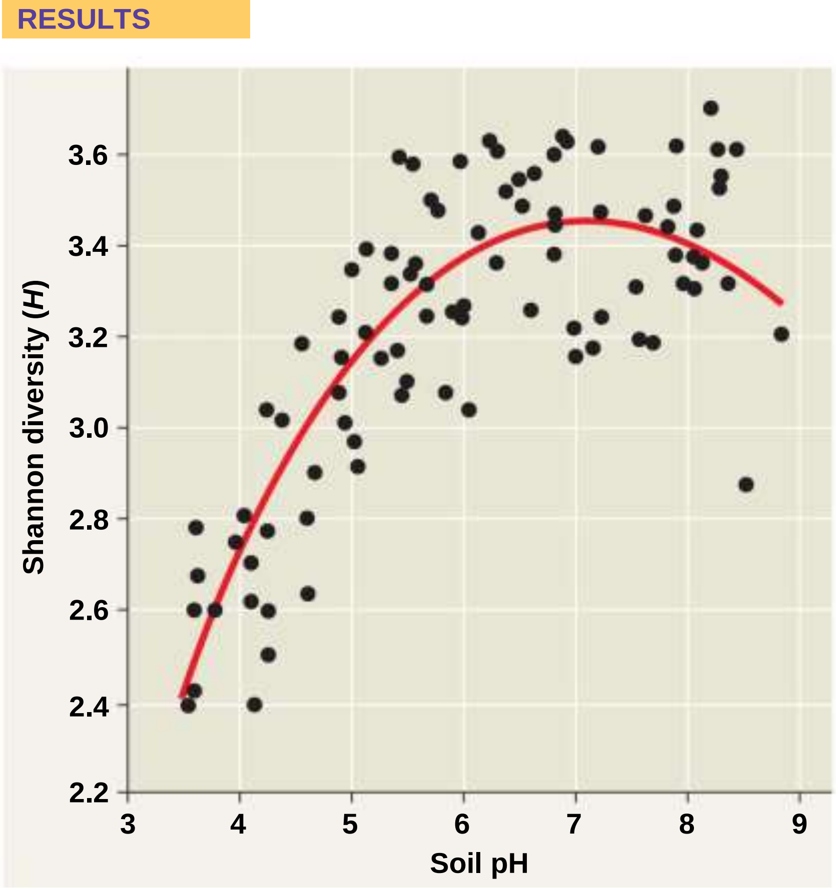


Community 1
A: 25% B: 25% C: 25% D: 25%

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

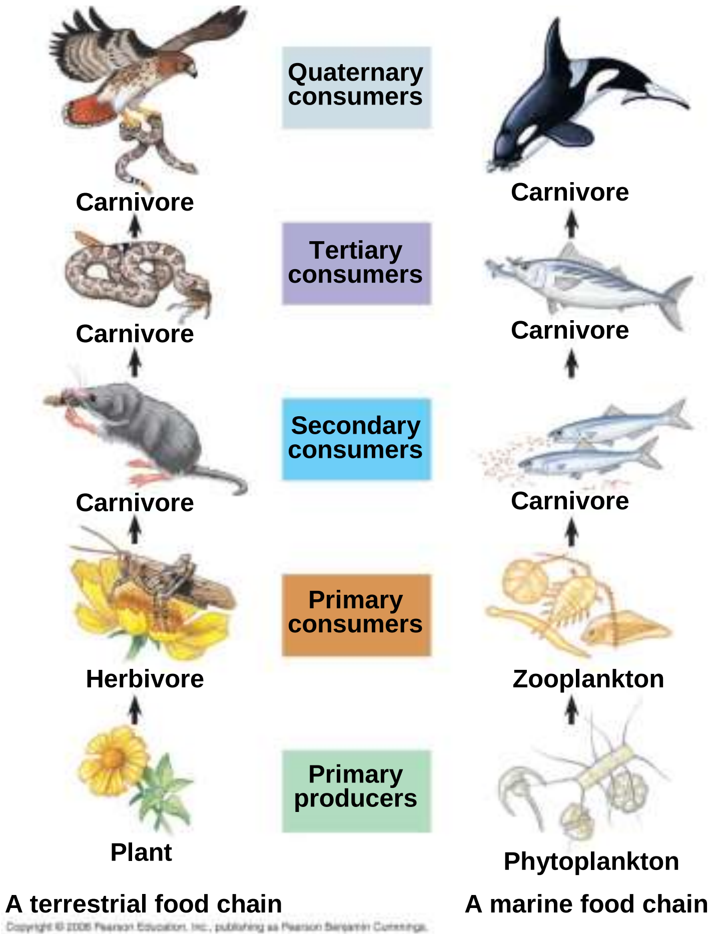
- Determining the number and abundance of species in a community is difficult, especially for small organisms
  - Molecular tools can be used to help determine microbial diversity
    - Ecologists often examine restriction fragment length polymorphisms (RFLPS) to produce a DNA fingerprint that can be used to identify different microbial species
      - They first extract and purify DNA from a specific portion of the microbial community (ex: soils of different pH)
      - PCR is then used to amplify the DNA, which is then labeled with a fluorescent dye
      - Restriction enzymes then cut the amplified, labeled DNA into fragments which are separated by gel electrophoresis

- The number and abundance of these fragments can then be used to determine species richness and relative abundance for different areas
  - Ex) Researchers determined that diversity of bacterial communities in soils across North and South America was related almost exclusively to soil pH
    - Shannon diversity is highest in neutral soils
    - Shannon diversity is lowest in acidic soils



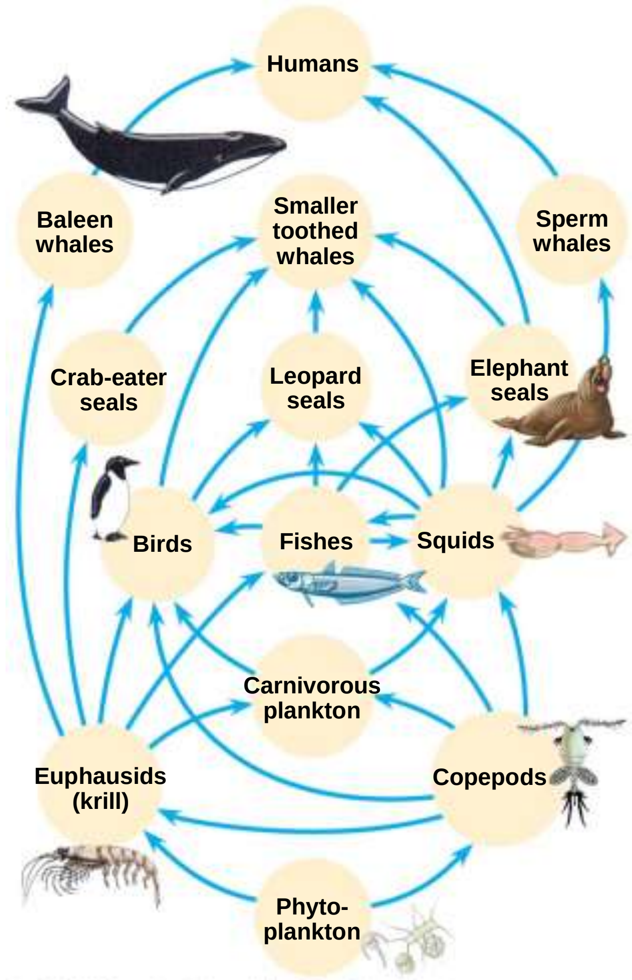
Trophic Structure

- Another fundamental feature of community structure and dynamics is feeding relationships between organisms, known as **trophic structure**
  - **Food chains** link trophic levels from producers to top carnivores
    - Food energy is transferred in the following manner:
      - Primary producers (plants and other autotrophic organisms)
      - Primary consumers (herbivores)
      - Secondary consumers (carnivores)
      - Tertiary consumers (carnivores)
      - Quaternary consumers (carnivores)
    - Decomposers "feed" on organisms from all trophic levels

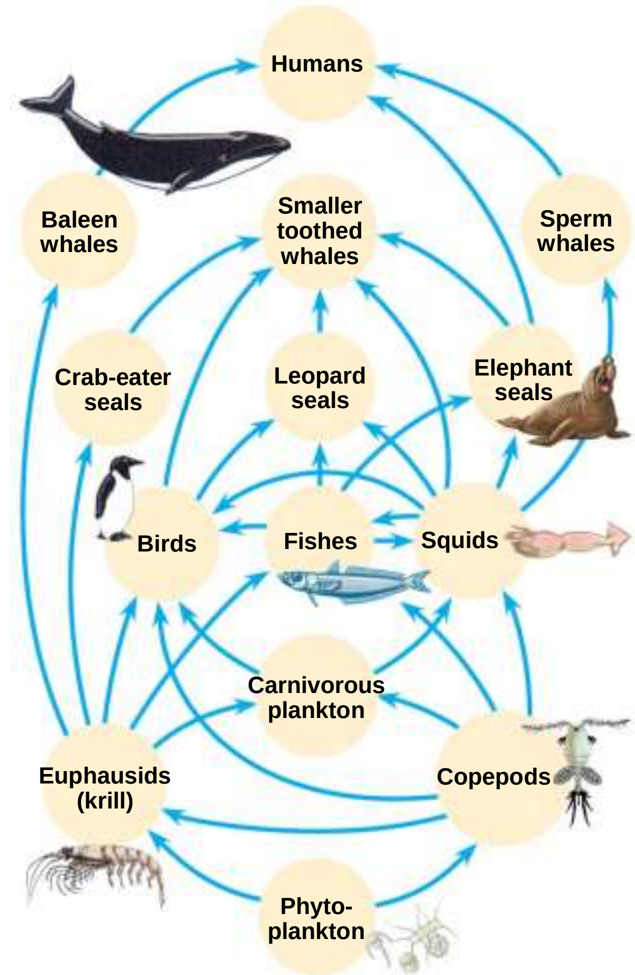


Food Webs

- Food chains are not isolated units, however
  - They can be linked together in food webs to summarize the trophic relationships of a community
    - A **food web** is a branching food chain with complex trophic interactions
  - In a food web, arrows link species according to who eats whom



- In the given food web of an antarctic pelagic community:
  - Primary producers: phytoplankton
  - Dominant primary consumers: zooplankton (krill and copepods)
  - Secondary consumers: carnivorous plankton, penguins, and fishes
  - Tertiary consumers: seals
  - Quaternary consumers: whales and humans
- Note: Depending on the specific food chain being examined, organisms can play a role at more than one trophic level
  - Ex) Squids are shown as both secondary and tertiary consumers



- Food webs can be very complicated, but they can be simplified for easier study in 2 ways:
  - Species with similar trophic relationships in a given community can be grouped into broad functional groups
    - Ex) More than 100 phytoplankton species are grouped together as primary producers in the previous food web
  - Portions of the web that interact very little with the rest of the community can be isolated
    - Ex) A partial food web is shown for the Chesapeake Bay estuary on the U.S. Atlantic coast

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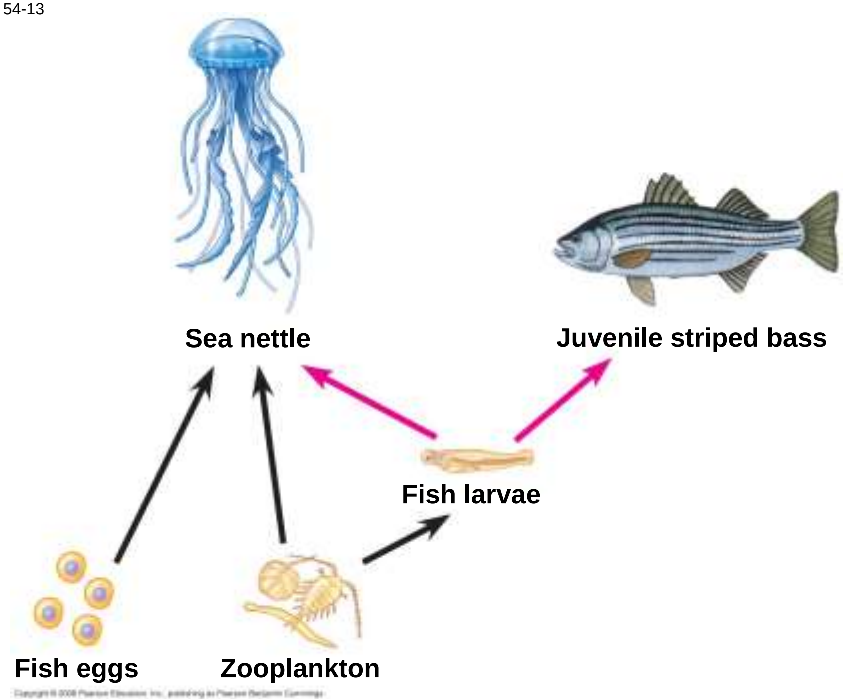
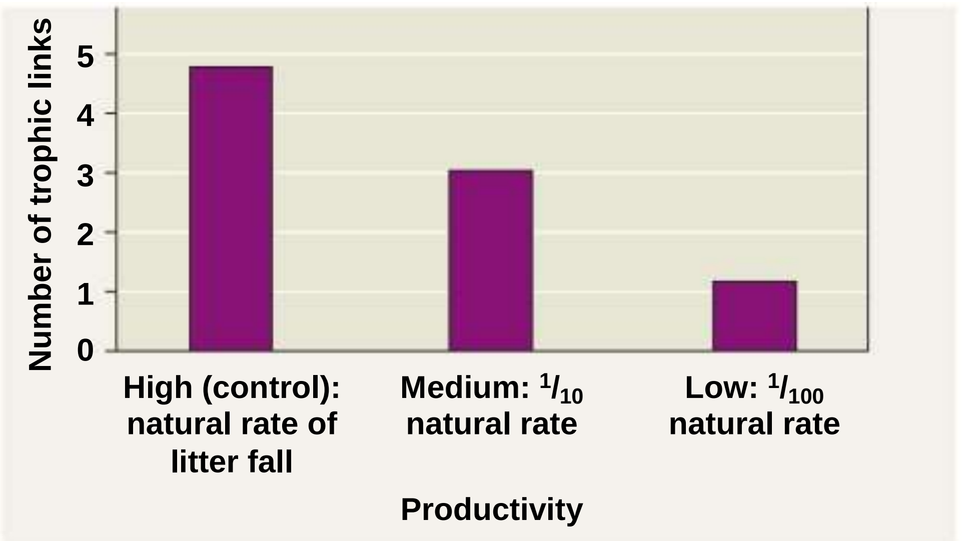


Limits on Food Chain Length

- Each food chain in a food web is usually only a few links long
  - There are rarely more than 7 links from producers to any top-level predator, with most chains containing fewer links
  - Two hypotheses attempt to explain food chain length: the energetic hypothesis and the dynamic stability hypothesis
    - The energetic hypothesis suggests that the length of a food chain is limited by the inefficiency of energy transfer along the chain
      - Only ~10% of the energy stored in organic matter of each trophic level is converted to organic matter at the next trophic level
        - Ex) 100 kg of plant material can support 10 kg of herbivore biomass (the total mass of all individuals in a population) and 1 kg of carnivore biomass
      - This hypothesis predicts that food chains should be relatively longer in habitats with higher photosynthetic production, which have a greater starting amount of energy

- The **dynamic stability hypothesis** proposes that long food chains are less stable than short ones
  - This is because population fluctuations at lower tropic levels are magnified at higher levels, which can potentially lead to local extinction of top predators
    - Predators at the top of the food chain must be able to recover from environmental shocks (ex: extreme winters) that reduce the food supply all the way up the food chain
    - The longer the food chain, the more slowly the top predators can recover from environmental setbacks
  - According to this hypothesis, food chains should also be shorter in unpredictable environments than in stable ones

- Most of the available data support the energetic hypothesis
  - Ecologists have used tree-hole communities in tropical forests as experimental models to test the energetic hypothesis
    - Many trees have small branch scars that rot, forming holes in the tree trunk
      - These tree holes hold water and provide a habitat for tiny communities of insects and microorganisms
    - Researchers manipulated productivity in these tree holes by controlling the amount of leaf litter falling into the tree holes
      - Holes with the most leaf litter, and therefore the greatest food supply at the producer level, supported the longest food chains



Species with a Large Impact

- Certain species have a very large impact on community structure, including:
  - Species that are highly abundant
    - Dominant species
  - Species that play a pivotal role in community dynamics
    - Keystone species
    - Foundation species
- Impacts of these species can occur through their trophic interactions or through their influences on the physical environment

Dominant Species

- **Dominant species** are those that are most abundant or have the highest biomass
  - Recall: Biomass is the total mass of all individuals in a population
- Dominant species exert powerful control over the occurrence and distribution of other species
  - There are several hypotheses to explain why a species becomes dominant in a community
    - One hypothesis suggests that dominant species are most competitively superior in exploiting limited resources, including water and nutrients
    - Another hypothesis is that they are most successful at avoiding predators or the impact of disease
      - This hypothesis is supported by observations of **invasive species**, which are typically introduced into a non-native environment by humans and therefore often lack natural predators or disease

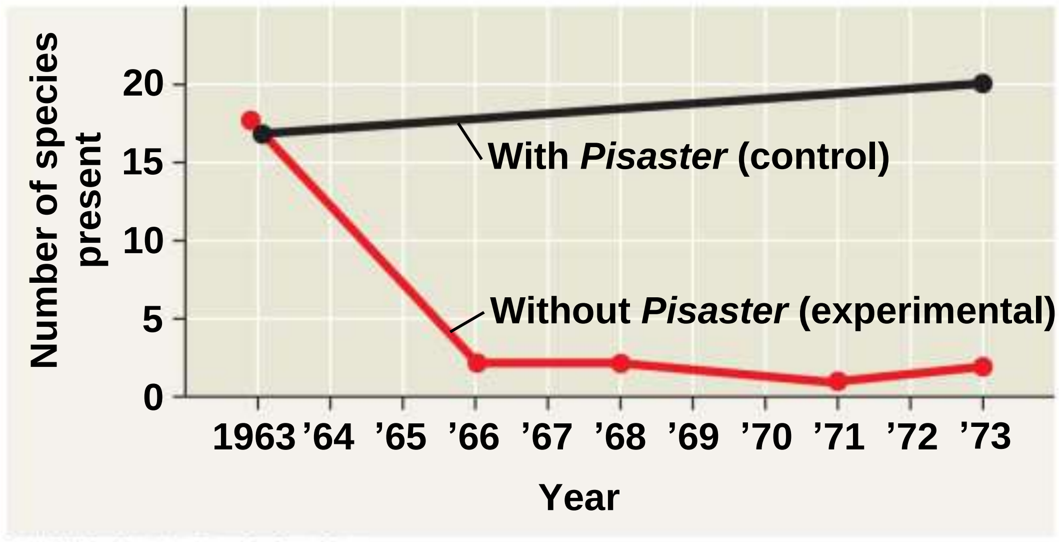
- One way to discover the impact of a dominant species is to remove it from the community
  - This type of experiment occurred accidentally with the American chestnut, a dominant tree in deciduous forests of eastern North America before 1910
    - Humans accidentally introduced a fungal disease via nursery stock imported from Asia
      - Between 1910 and 1950, this fungus killed all the chestnut trees in eastern North America
    - Some species in the community were relatively unaffected, while others were severely affected
      - Other trees, including oaks, hickories, beeches, and red maples, increased in abundance and replaced the chestnuts
      - No mammals or birds seemed to have been harmed by the loss of chestnuts
      - Seven species of moths and butterflies that fed on the tree became extinct

Keystone Species

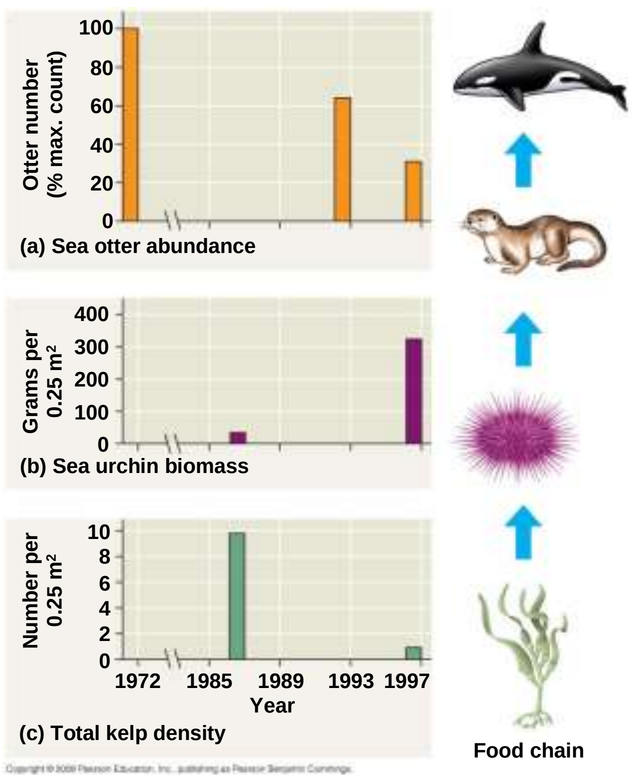
- **Keystone species** exert strong control on a community by their ecological roles, or niches
  - In contrast to dominant species, they are not necessarily abundant in a community
- Keystone species can be identified by removal experiments, such as those performed in a rocky intertidal community in western North America
  - Here, the sea star P. ochraceus, which is relatively low in abundance, preys on one of the dominant species in community, the mussel *M. californianus*
  - Researchers removed the sea star from an area in the intertidal zone and examined the resulting effects on species richness

- In the absence of the sea star, species richness declined
  - Mussels, who compete with the sea star for space, began monopolizing the rock face of the community
    - In doing so, the mussels eliminated most other invertebrates and algae
  - In the control area, where the sea star was not removed, species richness changed very little
- This experiment indicates that the sea star acts as a keystone species due to the influence it exerts on the community, even in low numbers

RESULTS



- Observations of sea otter populations and their predation provide another example of keystone species affect ocean communities
  - The sea otter is a keystone predator in the North Pacific, feeding on sea urchins, which in turn feed mainly on kelp
    - In areas where sea otters are abundant, sea urchins are rare and kelp forests are therefore well-developed
    - Where sea otters are rare, sea urchins are common and kelp is almost absent
  - Over the last 20 years, orcas have begun preying on sea otters as their usual prey declined in number
    - As a result, sea otter populations have declined by as much as 25% per year in large areas off the coast of western Alaska
      - The loss of the otters has allowed sea urchin populations to increase, resulting in the loss of kelp forests

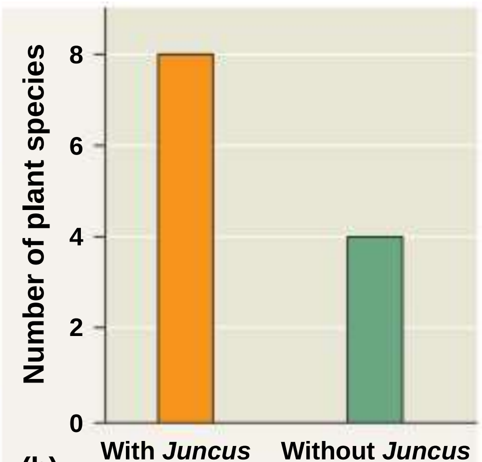


Foundation Species (Ecosystem "Engineers")

- Some species, known as foundation species (ecosystem "engineers") exert their influence on a community by causing physical changes in the environment
  - These changes can result from either their behavior or their large biomass
    - Ex) Beaver dams can transform landscapes on a very large scale

- Some foundation species may act as **facilitators** that have positive effects on survival and reproduction of some other species in the community
  - Ex) The black rush *J. gerardi* increases species richness in some zones of New England salt marshes
    - This plant prevents salt buildup in the soil by shading the soil surface, thus preventing evaporation
    - The black rush also prevents the salt marsh soils from becoming oxygen depleted as it transports oxygen to its below-ground tissues
  - Removal experiments of this foundation species suggest that the upper middle intertidal zone would support 50% fewer plant species in its absence

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



(b)

Bottom-Up and Top-Down Controls

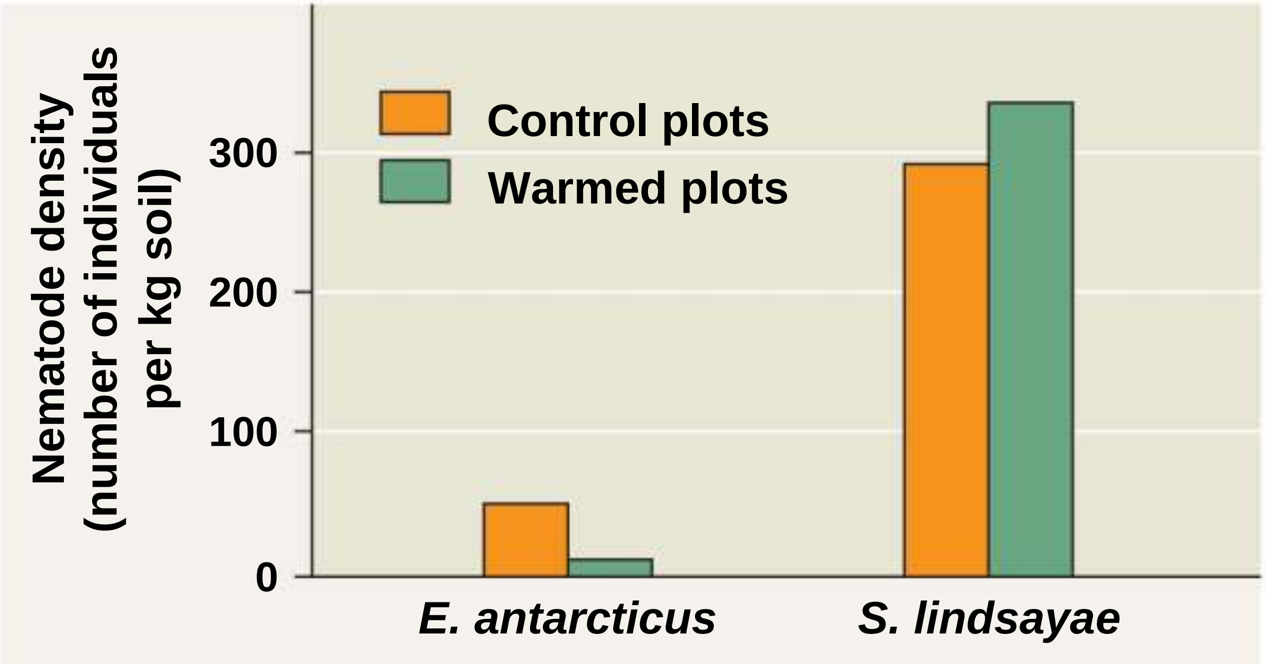
- Simplified models of relationships between adjacent trophic levels are useful for discussing community organization
  - Consider, for example, the 3 possible relationships between plants (V for vegetation) and herbivores (H)
    - The arrows below indicate that a change in the biomass of one trophic level causes a change in the other trophic level
      - $V \rightarrow H$: An increase in vegetation increases the biomass of herbivores, but not vice versa
      - $V \leftarrow H$: An increase in herbivore biomass decreases the abundance of vegetation, but not vice versa
      - $V \leftrightarrow H$: Both the plants and herbivores are sensitive to changes in the biomass of the other

- Two models of community organization are common: the bottom-up model and the top-down model
  - The **bottom-up model** of community organization proposes a unidirectional influence from lower to higher trophic levels
    - In this case, presence or absence of mineral nutrients (N) determines community structure, including abundance of primary producers (V), herbivores (H), and predators (P)
      - $N \rightarrow V \rightarrow H \rightarrow P$
    - In the case of the bottom-down model, changes in community structure will only occur if the biomass at the lower trophic levels is altered
      - These changes then propagate up through the food web
        - The addition of more mineral nutrients stimulates vegetation, which then allows higher trophic levels to increase in biomass
        - Addition or removal of predators from a bottom-down community, however, should not affect the lower trophic levels

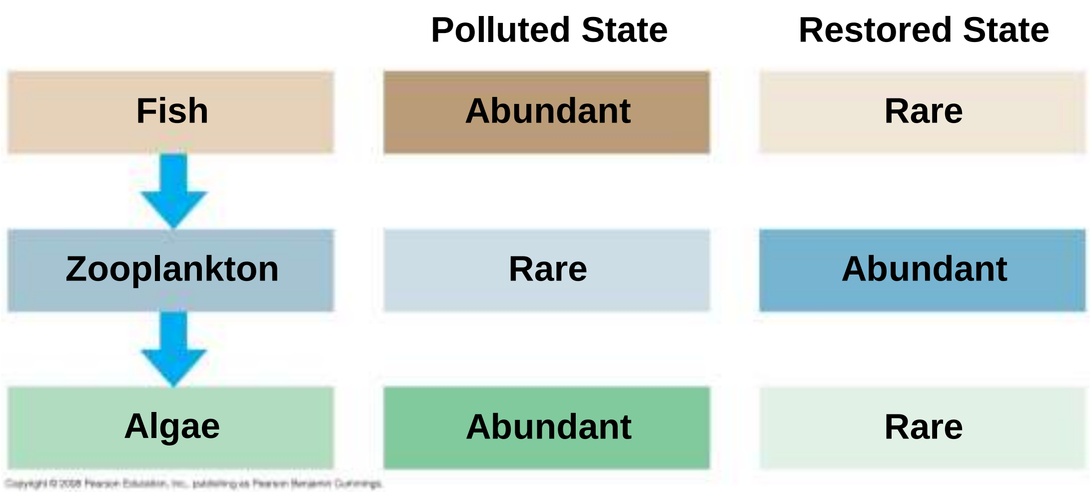
- The **top-down model**, also called the trophic cascade model, postulates the opposite
  - This model proposes that control comes from the trophic level above
    - In this case, predators control herbivores, which in turn control primary producers
      - $N \leftarrow V \leftarrow H \leftarrow P$
    - Any manipulation of trophic levels within a top-down ecosystem affect the trophic structure in a +/- manner
      - Ex) In a lake community with 4 trophic levels:
        - Removing top carnivores will increase the abundance of primary carnivores
        - In turn, this increase in primary carnivores decreases the number of herbivores
        - The decrease in herbivore number causes an increase in phytoplankton abundance
        - The increase in phytoplankton leads to decreasing concentrations of mineral nutrients

- Long-term experimental studies have shown that communities vary in their relative degree of bottom-up to top-down control
  - In one experiment, researchers investigated whether bottom-up or top-down factors are more important in a community of soil nematodes in the deserts of Antarctica
    - They chose this extreme environment because its nematode community contains only 2-3 species, making it easier to manipulate and study
  - ***Experiment:*** Researchers decreased the abundance of one predatory species of nematode *E. antarcticus* in selected plots by placing clear plastic chambers over the ground for one year, warming and drying the soil
    - Previous research had already shown that this species of nematode becomes less abundant under these conditions

- ***Results:*** The density of *E. antarcticus* in the warmed plots dropped to ¼ of the density in control plots
  - In contrast, the density of its prey species of nematode, *S. lindsayae* increased by 1/6
- ***Conclusion:*** The prey species' increase in density as the predatory density declined suggests that this soil nematode community is controlled by top-down factors



- The top-down model has been applied by ecologists to improve water quality in polluted lakes
  - This approach, called **biomanipulation**, attempts to prevent algal blooms and eutrophication by changing the density of higher-level consumers in lakes, rather than using chemical treatments
    - Ex) Removing fish from a lake should improve water quality by increasing zooplankton, thereby decreasing algal populations



Concept Check 54.2

- 1) What 2 components contribute to species diversity? Explain how 2 communities that contain the same number of species can differ in species diversity.
- 2) Describe 2 hypotheses that explain why food chains are usually short, and state a key prediction of each hypothesis.
- 3) Consider a grassland with 5 trophic levels: plants, grasshoppers, snakes, raccoons, and bobcats. If you released additional bobcats into the grassland, how would plant biomass change if the bottom-up model applied? If the top-down model applied?

Concept 54.3:
Disturbance influences species diversity and composition

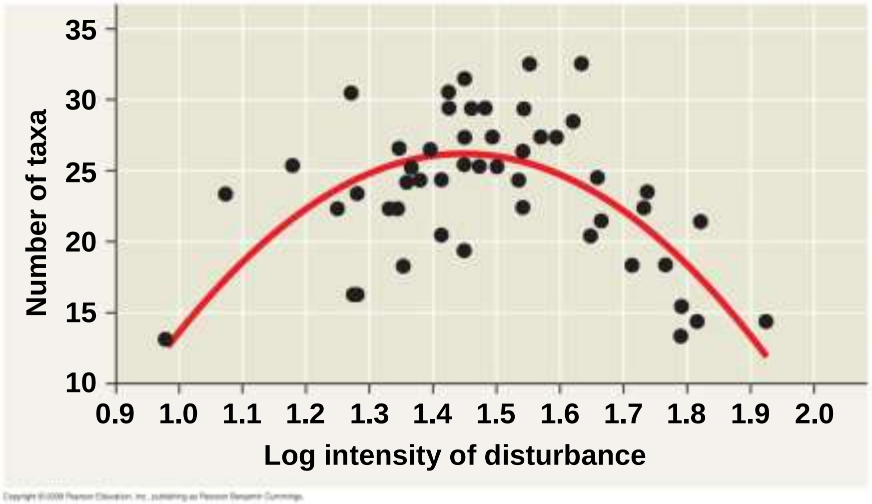
- Decades ago, most ecologists favored the view that communities are in a state of equilibrium (contain a relatively constant composition of species) unless seriously disturbed by human activity
  - Recent evidence, however, has led to a **nonequilibrium model**, which describes communities as constantly changing in the face of other, natural disturbances
    - **Disturbances** are any events that change a community by removing organisms from it or altering resource availability
      - Storm
      - Fire
      - Flood
      - Drought
      - Overgrazing
      - Human activity

Characterizing Disturbance

- The types of disturbances and their frequency and severity vary from community to community
  - Storms disturb almost all communities, even those in oceans due to wave action
  - Fire is a significant disturbance in most terrestrial ecosystems
    - It is often a necessity in some communities, including chaparral and some grassland biomes, to maintain their structure and species composition
  - Freezing is another type of frequent disturbance in many rivers, lakes, and ponds
    - Many of these streams and ponds are also disturbed by spring flooding and seasonal drying
- A high level of disturbance is generally the result of high intensity AND frequency of disturbance
  - Low disturbance levels can result from either low intensity or low frequency of disturbance

- The **intermediate disturbance hypothesis** suggests that moderate levels of disturbance can foster greater species diversity than either high or low levels of disturbance
  - High levels of disturbance reduce species diversity by creating environmental stresses that exceed the tolerance of many species or by excluding many slow-growing species
  - Low levels of disturbance can reduce species diversity by allowing dominant species to exclude less competitive species
  - Meanwhile, intermediate levels of disturbances can increase species diversity by opening up habitats for occupation by less competitive species
    - In addition, the moderate disturbance levels rarely create environmental conditions severe enough to exceed the tolerances or rate of recovery by community members

- The intermediate disturbance hypothesis is supported by many terrestrial and aquatic studies
  - Ex) Ecologists in New Zealand compared the species richness of invertebrate taxa living in the beds of streams exposed to different frequencies and intensities of flooding
    - When floods occurred either very frequently or rarely, invertebrate richness was low
      - Frequent floods made it difficult for some species to become established in the streambed
      - Rare floods resulted in species being displaced by superior competitors
    - Invertebrate richness peaked in streams that had an intermediate frequency or intensity of flooding



- Though moderate levels of disturbance maximize species diversity, small and large disturbances can also have important effects on community structure
  - The large-scale fire in Yellowstone National Park in 1988 demonstrated that communities can often respond very rapidly to a massive disturbance
    - Much of the preserve is dominated by lodgepole pines, which require periodic fires to open their cones and release their seeds
      - The new generation of pines then thrives on nutrients released by the burned trees and in the sunlight that is no longer blocked by taller trees
    - In 1988, however, extensive areas were burned during a severe drought
      - By 1989, burned areas in the park were largely covered with new vegetation, suggesting that this community's species adapted to rapid recovery after fire
        - This also supports the nonequilibrium model of community structure

(a) Soon after fire

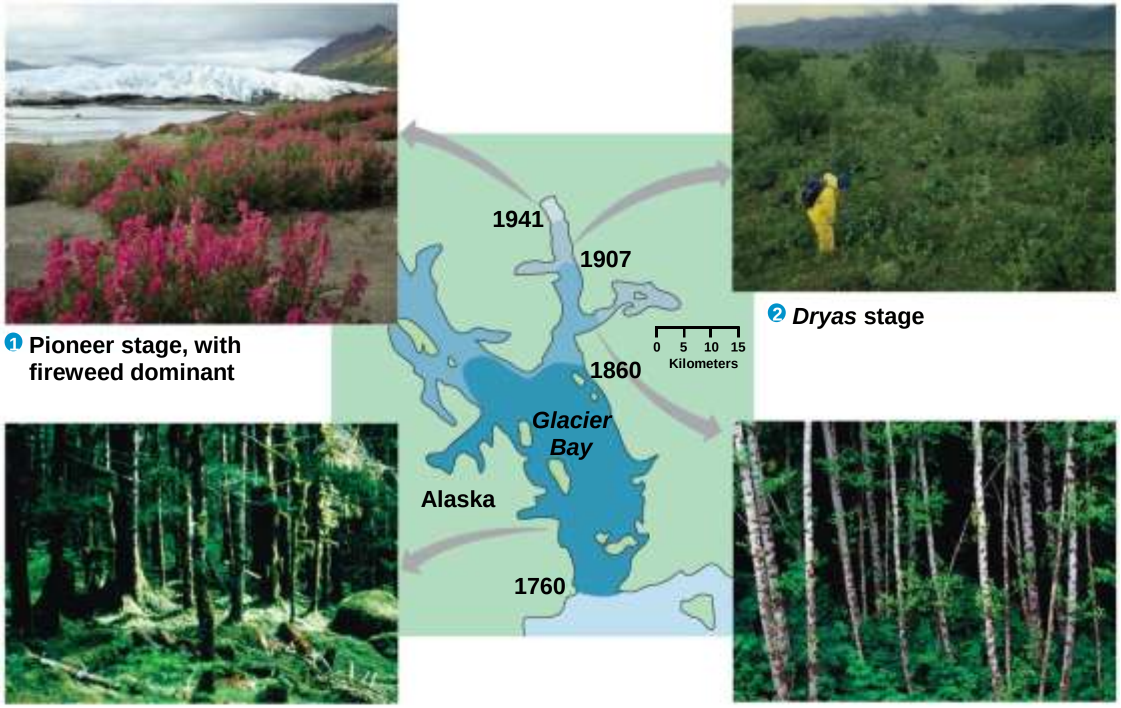
(b) One year after fire

Ecological Succession

- **Ecological succession** is the sequence of community and ecosystem changes after a disturbance
  - Depending on the presence or absence of soil, and therefore the presence of living communities of organisms, ecological succession can be categorized as either primary or secondary succession
- **Primary succession** occurs where no soil exists when succession begins
    - Ex) New volcanic island or the rubble (moraine) left by a retreating glacier
  - The only life forms typically present at first are prokaryotes and protists
    - Lichens and mosses are most commonly the first macroscopic photosynthesizers to colonize these areas
  - Soil develops gradually as rocks weather and organic matter accumulates from the decomposed remains of early colonizers
    - Once soil is present, grasses, shrubs, and trees usually overgrow the lichens and mosses
  - Eventually, the area is colonized by plants that become the community's prevalent form of vegetation
    - Producing such communities through primary succession takes 100s-1000s of years

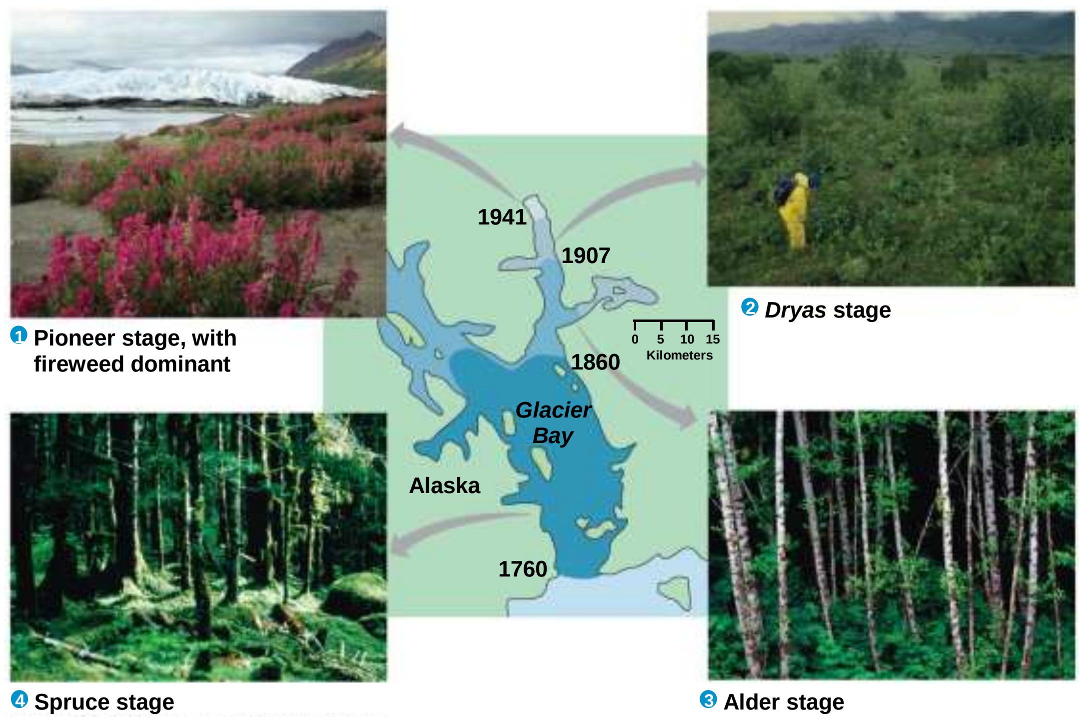
- **Secondary succession** begins in an area where soil remains after a disturbance
    - Ex) Yellowstone National Park following the 1988 fires
  - The order in which particular species arrive may be linked in one of three key processes
    - The early arrivals may *facilitate* the appearance of later species by making the environment more favorable
    - The early species may *inhibit* establishment of the later species
    - The early species may be completely independent of the later species, which *tolerate* conditions created early in succession but are *neither helped nor hindered* by early species

- Retreating glaciers provide a valuable field-research opportunity for observing succession
  - Primary succession on the moraines in Glacier Bay, Alaska, follows a predictable pattern of change in vegetation and soil characteristics
    - By studying the communities on moraines at different distances from the mouth of the bay, ecologists can examine different stages in succession
- 1) The exposed moraine is colonized first by pioneering species, including liverworts, mosses, fireweed, scattered *Dryas* (a mat-forming shrub), willows, and cottonwood



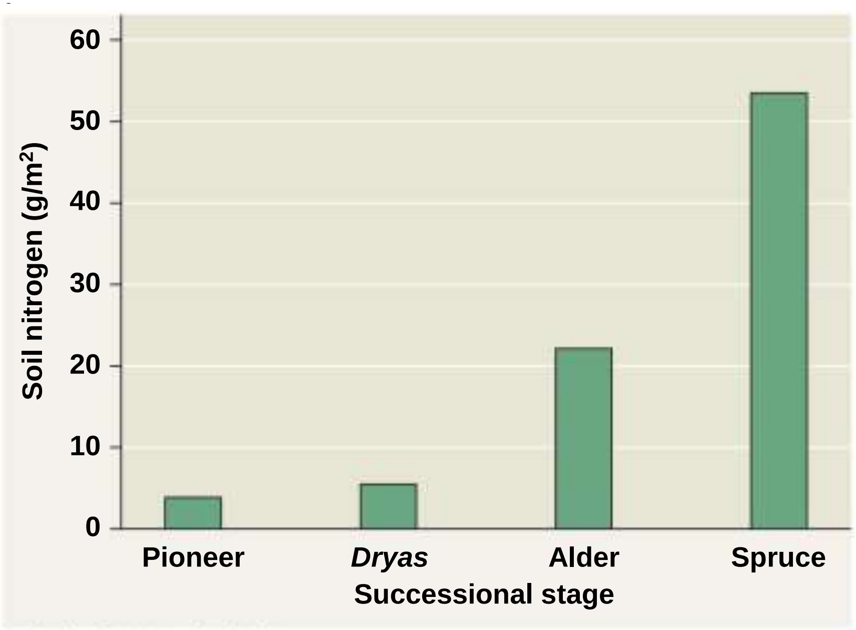
1 Pioneer stage, with fireweed dominant
2 *Dryas* stage
3 Alder stage
4 Spruce stage

- 2) After ~3 decades, *Dryas* dominates the plant community
- 3) A few decades later, the area is invaded by alder, which forms dense thickets up to 9 meters tall
- 4) In the next 2 centuries, the alder stands are overgrown first by Sitka spruce and later by a combination of western and mountain hemlock
  - In areas of poor drainage, the forest floor of this spruce-hemlock forest is invaded by sphagnum moss
    - The moss holds large amounts of water and acidifies the soil, eventually killing the trees
    - Therefore, after ~300 years, the vegetation consists of sphagnum bogs on poorly-drained flat areas and spruce-hemlock forest on the well-drained slopes



- Succession is the result of changes induced by the vegetation itself
  - On the glacial moraines, vegetation lowers the soil pH
    - The bare soil exposed as the glacier retreats is very basic (pH = 8.0 – 8.4) due to carbonate compounds in the parent rocks
      - The soil pH falls rapidly as vegetation develops, particularly after decomposition of acidic spruce needles, which drop the soil pH down to around 4.0

- The bare soil after glacial retreat is also low in nitrogen content
  - As a result, almost all pioneer plant species begin succession with poor growth and yellow leaves
    - *Dryas* and alder are two exceptions, since both contain symbiotic bacteria that fix atmospheric nitrogen
  - Soil nitrogen content increases rapidly during the alder stage of succession and continues to increase during the spruce stage
- Thus, pioneer plant species permit new plant species to grow by altering soil properties
  - These new plants, in turn, then alter the environment in different ways, further contributing to succession



Human Disturbance

- One of the strongest agents of disturbance today is human activity
  - Human disturbance to communities usually reduces species diversity
    - Agricultural development has disrupted vast grasslands once present on the North American prairies
    - Logging and clearing for urban development, mining, and farming have reduced large forests to small patches of disconnected woodlots
      - Tropical rain forests are also quickly disappearing as a result of clear-cutting for lumber, cattle grazing, and farmland
    - Marine ecosystems are also being cleared as they are scraped and scoured by weighted nets dragged by boats across the seafloor

54.3 Concept Check

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

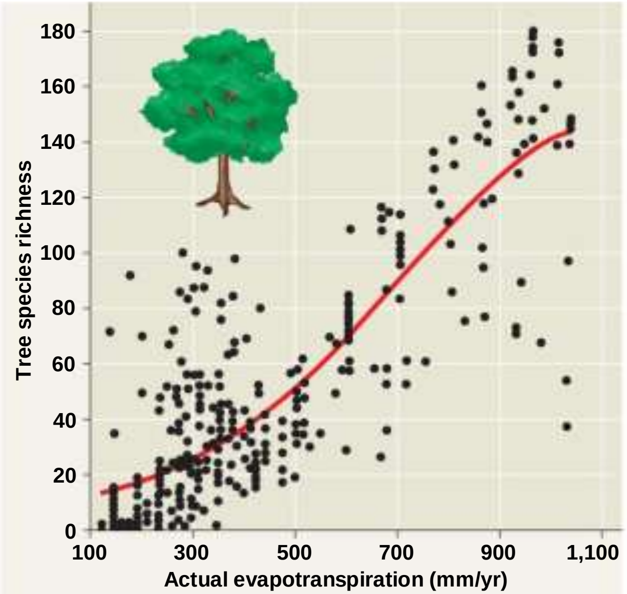
Concept 54.4:
Biogeographic factors affect community biodiversity

- In addition to small-scale or local factors, large-scale biogeographic factors also contribute to species diversity in biological communities
  - Two such key factors that affect a community's species diversity are:
    - Latitude
    - Area

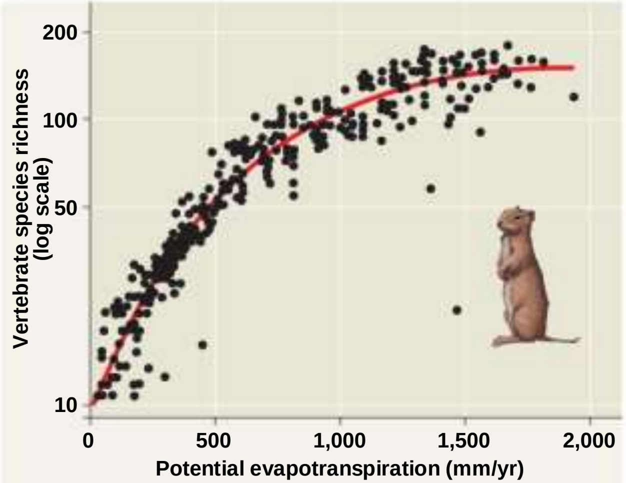
Latitudinal Gradients

- Species richness generally declines along an equatorial-polar gradient and is especially great in the tropics
  - Two key factors in these equatorial-polar gradients of species richness are probably (1) evolutionary history and (2) climate
    - 1) The greater age of tropical environments may account for the greater species richness
      - Tropical communities are generally older than temperate or polar communities because their growing season is ~5X as long
        - As a result, biological time and hence intervals during speciation events runs ~5X as fast in the tropics than near the poles
        - In addition, many polar and temperate communities have repeatedly “started over” due to major disturbances, including glaciation

- 2) Climate is probably the main cause of the latitudinal gradient in biodiversity
  - Two main climatic factors correlated with biodiversity are solar energy and water availability
    - Where these resources are abundant (ex: tropics), species richness tends to be high
  - Solar energy and water availability can be considered together by measuring a community’s rate of evapotranspiration
    - **Evapotranspiration** is evaporation of water from soil plus transpiration of water from plants
    - *Potential evapotranspiration* is a measure of the potential water loss due to solar radiation and temperature, assuming water is readily available
  - Evapotranspiration is much higher in hot areas with abundant rainfall than in areas with low temperatures or precipitation



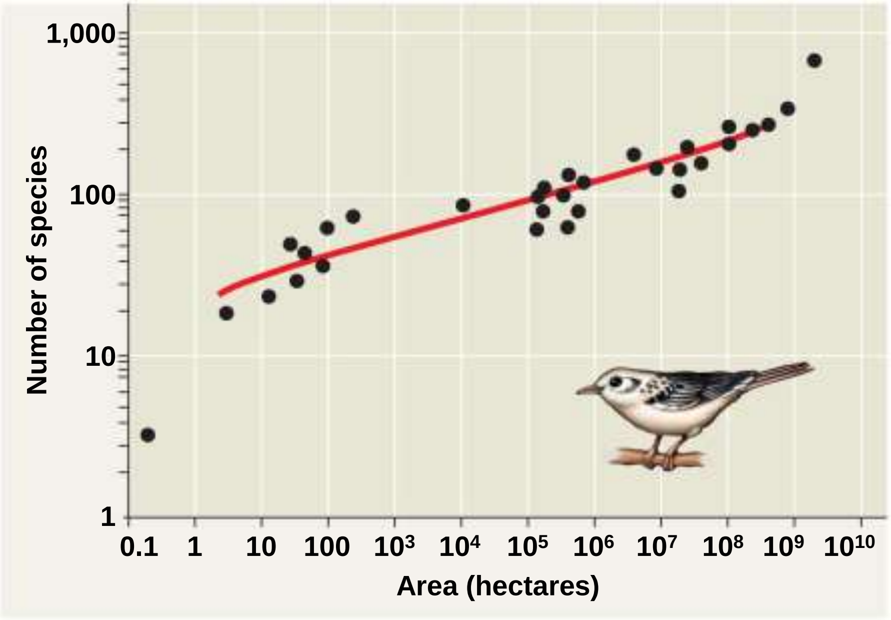
(a) Trees



(b) Vertebrates

Area Effects

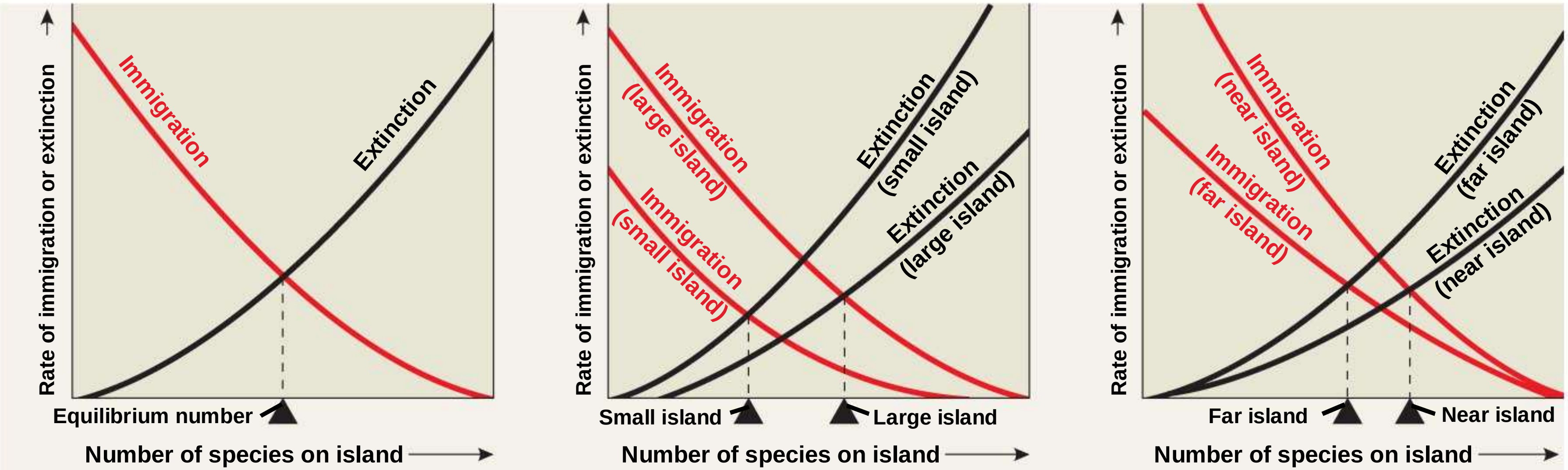
- The **species-area curve** quantifies the idea that, all other factors being equal, a larger geographic area has more species
  - The most probable explanation for this pattern is that larger areas offer a greater diversity of habitats than smaller areas
    - A species-area curve of North American breeding birds (as opposed to migrant populations) supports this idea



- Islands provide excellent opportunities for studying biogeographic factors that affect a community's species diversity
  - An "island" can be defined as any patch of habitat surrounded by an environment not suitable for the "island" species
    - Ex) Mountain peaks and lakes
- Consider a newly formed oceanic island that receives colonizing species from a distant mainland
  - Species richness on this island depends on 4 factors:
    - Island size: small (less visible) islands generally have lower immigration rates because potential colonizers are less likely to reach them than large islands
    - Distance from the mainland: closer islands generally have higher immigration rates
    - Immigration: as immigration rate increases, extinction rates increase because of the greater chance of competitive exclusion
    - Extinction: smaller islands have higher extinction rates because they contain fewer resources and less diverse habitats available for partitioning

Island Equilibrium Model

- The equilibrium model of island biogeography maintains that species richness on an ecological island levels off at a dynamic equilibrium point
  - According to this model, the rate of species immigration will eventually equal the rate of species extinction
    - The number of species at this equilibrium point is further correlated with the island's size and distance from mainland

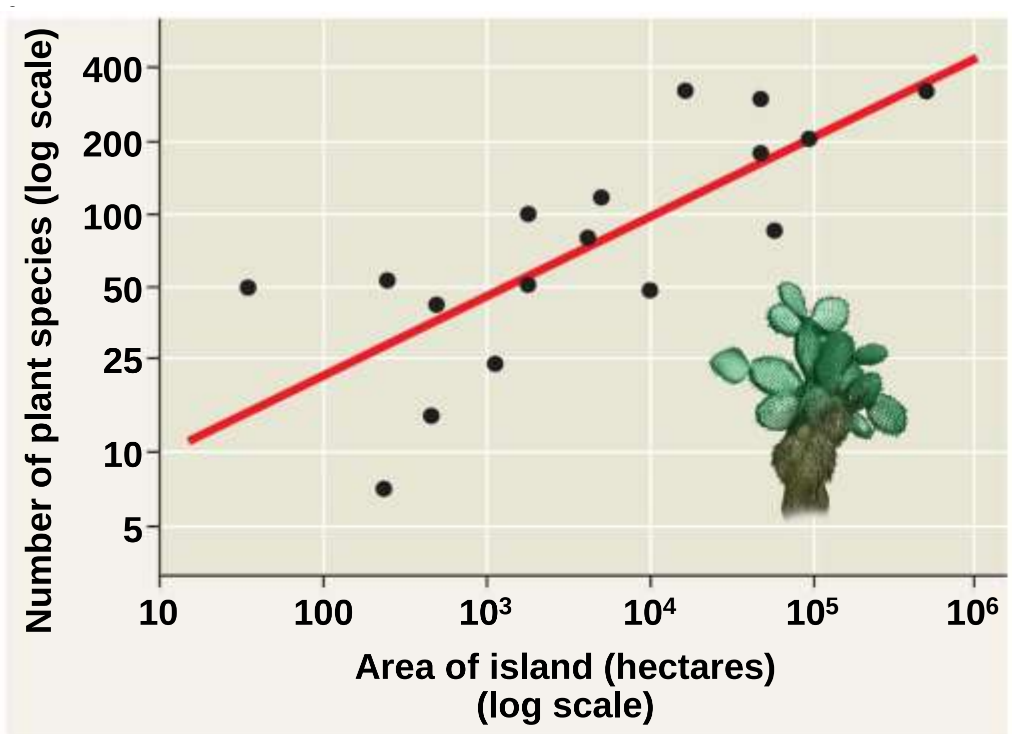


(a) Immigration and extinction rates

(b) Effect of island size

(c) Effect of distance from mainland

- Studies of species richness on the Galápagos Islands support the prediction that species richness increases with island size
    - Species abundance also fits the prediction that the number of species decreases with increasing remoteness (distance) of the island



Concept Check 54.4

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

Concept 54.5:
Community ecology is useful for understanding pathogen life cycles and controlling human disease

- Ecological communities are also universally affected by **pathogens**, which include:
  - Disease-causing microorganisms
  - Viruses
  - Viroids (infectious RNA molecules)
  - Prions (infections proteins)
- Pathogens can alter community structure quickly and extensively

Pathogens and Community Structure

- Pathogens can have dramatic effects on communities
  - For example, coral reef communities are being decimated by white-band disease
    - This disease kills corals by causing their tissue to slough off in a band from the base to the tip of the branches
      - As a result of this disease, many species of corals have been decimated since the 1980s

    - When these corals die, they are quickly overgrown by algae
      - As a result, herbivores that feed on this algae come to dominate the fish community
    - Eventually, the corals topple due to disturbances including storms
      - This, in turn, decreases species diversity further, since corals provide key habitats for lobsters and many fish species

- Pathogens also influence community structure in terrestrial ecosystems
  - Trees of several species are dying from sudden oak death (SOD) in the forests and savannahs of California
    - This disease is caused by a fungus-like protist called *P. ramorum*
  - The loss of more than 1 million oaks and other trees from the central California coast to southern Oregon has led to a decrease in the abundance of at least 5 bird species

Community Ecology and Zoonotic Diseases

- Three-quarters of today's emerging human diseases are caused by zoonotic pathogens
  - **Zoonotic** pathogens are those that have been transferred from other animals to humans
    - Some examples include mad cow disease and malaria
  - The transfer of these pathogens can be through direct contact with an infected animal or through an intermediate species, called a **vector**
    - Some common vectors include ticks, lice, and mosquitoes

- Understanding parasite life cycles allows scientists to devise ways to control and track the spread of zoonotic diseases
  - For example, ecologists are studying the potential spread of avian flu, a highly contagious virus of birds, from Asia to North America through migrating birds
    - Since 2003, one particular strain of this virus (H5N1), has killed millions of poultry and more than 150 people
  - Control programs that quarantine domestic birds or monitor their transport may be ineffective if the avian flu spreads naturally through the movement of wild birds
    - Ecologists are currently studying the potential spread of this virus into the U.S. by trapping and testing migrating and resident birds in Alaska
      - Alaska is the most likely place for infected wild birds to enter the Americas as they migrate across the Bering Sea from Asia each year

Concept Check 54.5

- 1) What are pathogens?
- 2) Some parasites require contact with at least 2 host species to complete their life cycle. Why might this characteristic be important for the spread of certain zoonotic diseases?
- 3) Suppose a new zoonotic disease emerges from a tropical rain forest. Doctors have no way yet to treat the disease, so preventing infections is particularly important. As a community ecologist, how might you help prevent the spread of the disease?

You should now be able to:

1. Distinguish between the following sets of terms: competition, predation, herbivory, symbiosis; fundamental and realized niche; cryptic and aposematic coloration; Batesian mimicry and Müllerian mimicry; parasitism, mutualism, and commensalism; endoparasites and ectoparasites; species richness and relative abundance; food chain and food web; primary and secondary succession

2. Define an ecological niche and explain the competitive exclusion principle in terms of the niche concept
3. Explain how dominant and keystone species exert strong control on community structure
4. Distinguish between bottom-up and top-down community organization
5. Describe and explain the intermediate disturbance hypothesis

6. Explain why species richness declines along an equatorial-polar gradient
7. Define zoonotic pathogens and explain, with an example, how they may be controlled