CAMPBELL BIOLOGY IN FOCUS

URRY • CAIN • WASSERMAN • MINORSKY • REECE

41

Species Interactions

Lecture Presentations by
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SECOND EDITION

Communities in Motion

- A biological **community** is an assemblage of populations of various species living close enough for potential interaction
  - For example, the "carrier crab" carries a sea urchin on its back for protection against predators

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

- Ecologists call relationships between species in a community **interspecific interactions**
- Examples are competition, predation, herbivory, parasitism, mutualism, and commensalism
- Interspecific interactions can affect the survival and reproduction of each species, and the effects can be summarized as positive (+), negative (–), or no effect (0)

Competition

- **Interspecific competition** (−/− interaction) occurs when species compete for a resource that limits their growth or survival

Competitive Exclusion

- Strong competition can lead to **competitive exclusion**, local elimination of a competing species
- The competitive exclusion principle states that two species competing for the same limiting resources cannot permanently coexist in the same place

Ecological Niches and Natural Selection

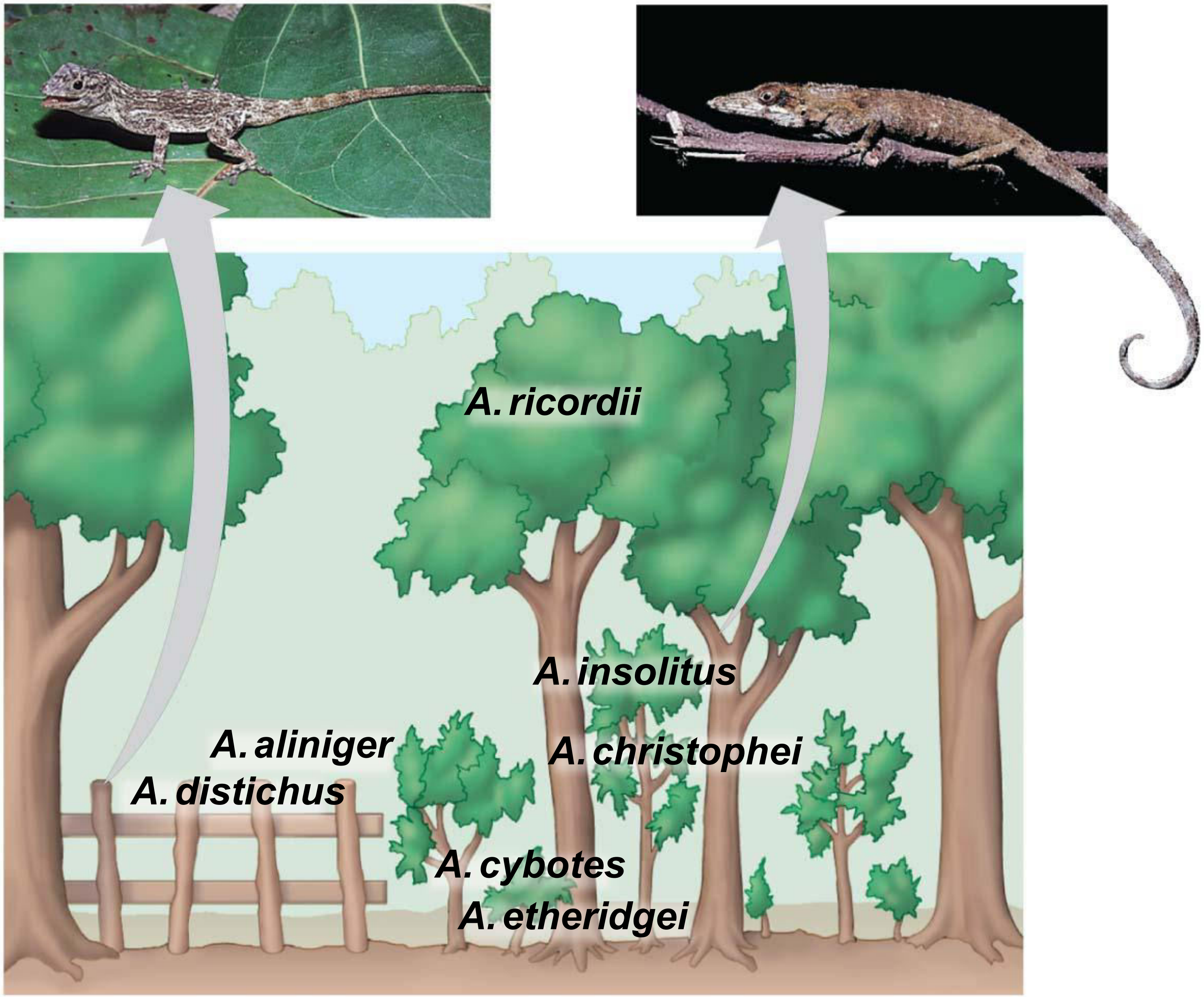
- Evolution is evident in the concept of the **ecological niche**, the specific set of biotic and abiotic resources used by an organism
- An ecological niche can also be thought of as an organism’s ecological role
- Ecologically similar species can coexist in a community if there are one or more significant differences in their niches

- **Resource partitioning** is differentiation of ecological niches, enabling similar species to coexist in a community

Figure 41.2

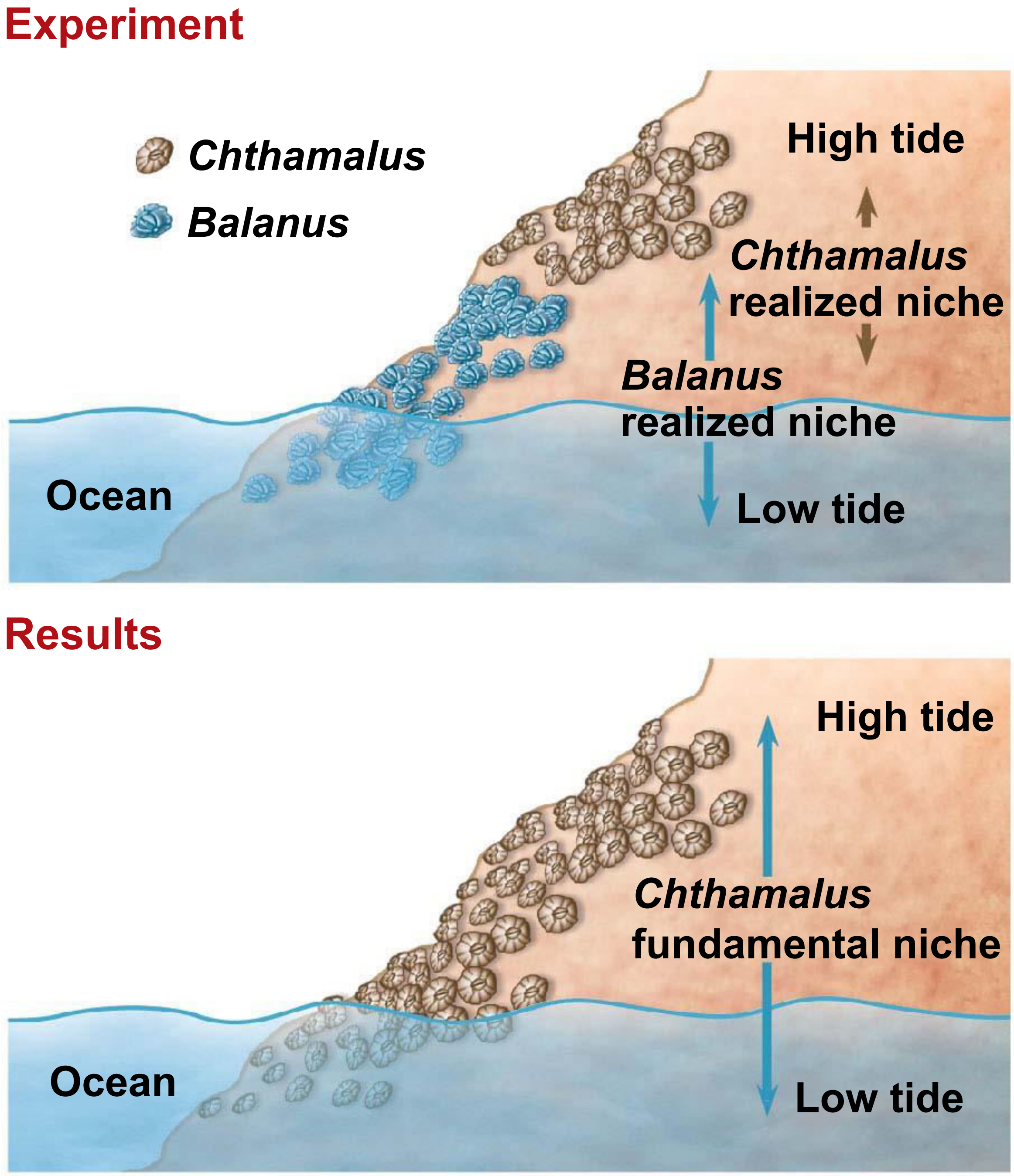
A. distichus perches on fence posts and other sunny surfaces.

A. insolitus usually perches on shady branches.



- A species' fundamental niche is the niche potentially occupied by that species
- A species' realized niche is the niche actually occupied by that species
- As a result of competition, a species' fundamental niche may differ from its realized niche
  - For example, the presence of one barnacle species limits the realized niche of another species

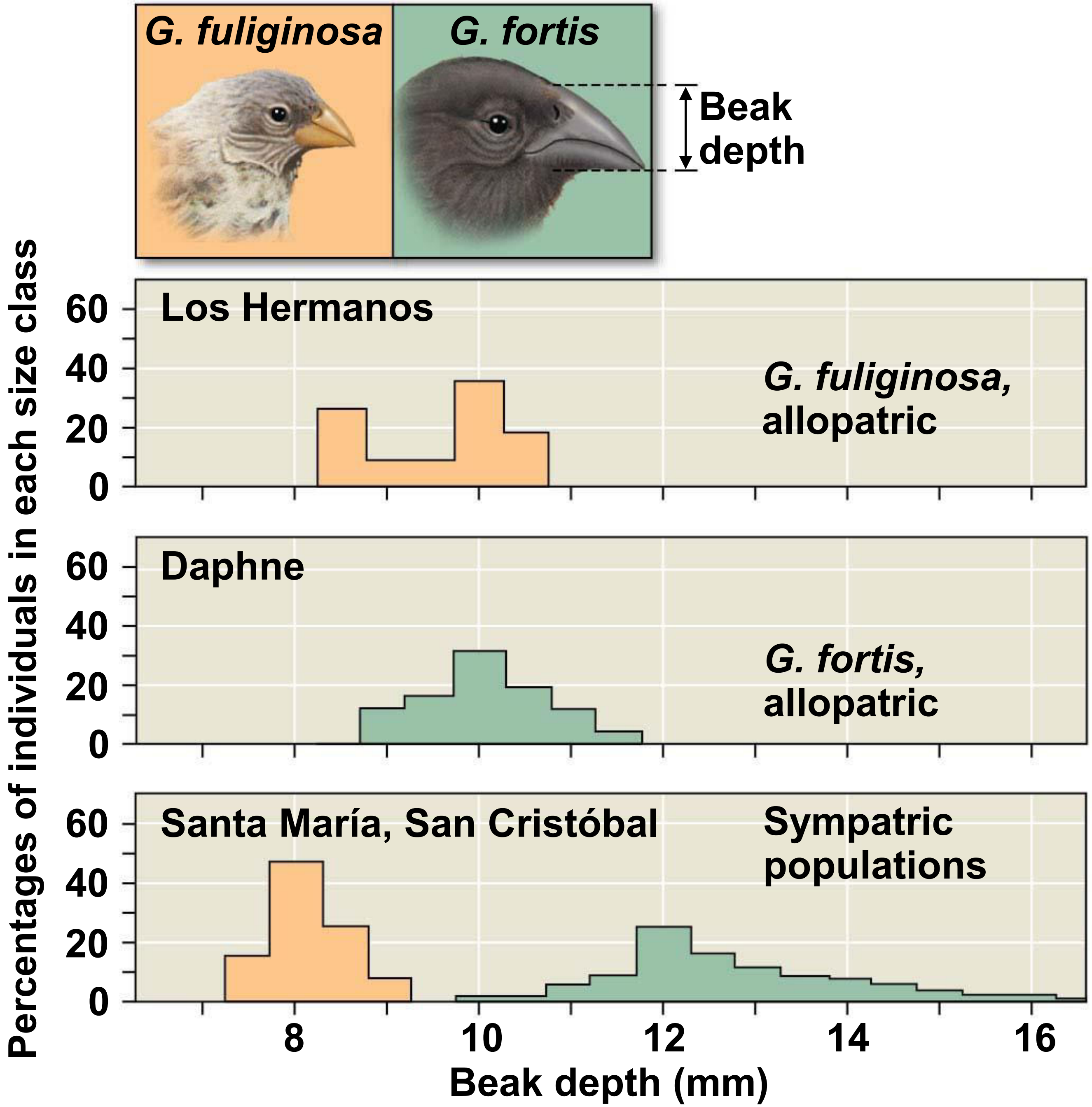
Figure 41.3


Experiment
Chthamalus
Balanus
High tide
Chthamalus
realized niche
Balanus
realized niche
Ocean
Low tide
Results
High tide
Chthamalus
fundamental niche
Ocean
Low tide

Character Displacement

- **Character displacement** is a tendency for characteristics to be more divergent in sympatric populations of two species than in allopatric populations of the same two species
- An example is variation in beak size between populations of two species of Galápagos finches

Figure 41.4


G. fuliginosa
G. fortis
Beak depth
Los Hermanos
G. fuliginosa, allopatric
Daphne
G. fortis, allopatric
Santa María, San Cristóbal
Sympatric populations
Percentages of individuals in each size class
60
40
20
0
8
10
12
14
16
Beak depth (mm)

Exploitation

- **Exploitation** refers to any +/– interaction in which one species benefits by feeding on the other, while the other species is harmed
- Predation, herbivory, and parasitism are exploitative interactions

Predation

- **Predation** (+/– interaction) refers to an interaction in which one species, the predator, kills and eats the other, the prey
- Predators have acute senses for locating prey, such as the heat-sensing organs used by pit vipers
- Some predator adaptations for capturing prey include claws, fangs, and poison

- Prey display various defensive adaptations
- Behavioral defenses include hiding, fleeing, forming herds or schools, and active self-defense
- Animals also have morphological and physiological defense adaptations
- **Cryptic coloration**, or camouflage, makes prey difficult to spot

- Animals with effective chemical defenses often exhibit bright warning coloration, called **aposematic coloration**
- Predators tend to avoid prey that display such coloration

- In some cases, a prey species may gain significant protection by mimicking the appearance of another species
- In **Batesian mimicry**, a palatable or harmless species mimics an unpalatable or harmful model
- Predators also use mimicry to attract or sneak up on prey

Figure 41.5

(a) Cryptic coloration

▶ **Canyon tree frog**

(b) Aposematic coloration

▶ **Poison dart frog**

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

◀ **Nonvenomous hawkmoth larva**

▼ **Venomous green parrot snake**

Herbivory

- **Herbivory** (+/– interaction) refers to an interaction in which an herbivore eats parts of a plant or alga
- Large mammalian herbivores are most familiar, but most herbivores are small invertebrates
- In marine communities, sea urchins, fish, and some mammals, such as the manatee, are herbivorous

- Herbivores have adaptations, such as chemical sensors and specialized teeth or digestive systems, for seeking and feeding on prey
- Plant defenses include chemical toxins and protective structures, such as spines and thorns

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**
- Parasites that live on the external surface of a host are **ectoparasites**

- Many parasites have a complex life cycle involving multiple hosts
- Some parasites change the behavior of the host in a way that increases the parasites' fitness
- Parasites can significantly affect survival, reproduction, and density of host populations, either directly or indirectly

Positive Interactions

- **Positive interactions** refer to any +/+ or +/0 interaction in which at least one species benefits and neither is harmed
- Mutualism and commensalism are positive interactions

Mutualism

- **Mutualism** (+/+ interaction), is an interspecific interaction that benefits both species
- In some mutualisms, one or both species cannot survive without the other
  - For example, acacia trees and ants are dependent upon each other for survival and reproduction
- In other mutualisms, both species can survive alone

Figure 41.7

(a) Ants (genus *Pseudomyrmex*) in acacia tree

(b) Area cleared by ants around an acacia tree

Figure 41.7-1

(a) Ants (genus *Pseudomyrmex*) in acacia tree

(b) Area cleared by ants around an acacia tree

- Each partner in a mutualistic interaction experiences a cost, but the benefits of the interaction exceed the costs to the participants

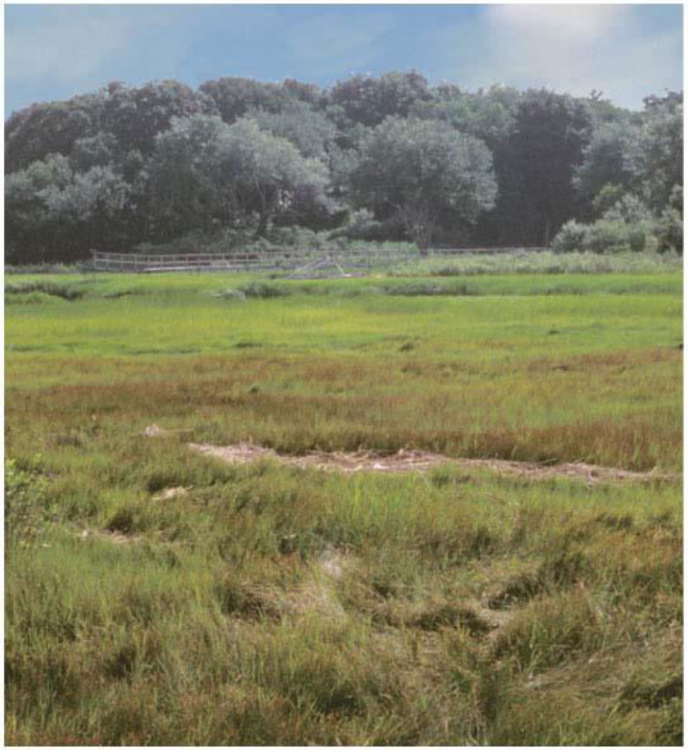
Commensalism

- In **commensalism** (+/0 interaction), one species benefits and the other is neither harmed nor helped
  - For example, some wildflowers benefit from the habitat provided by forest trees, but do not affect the trees in any way

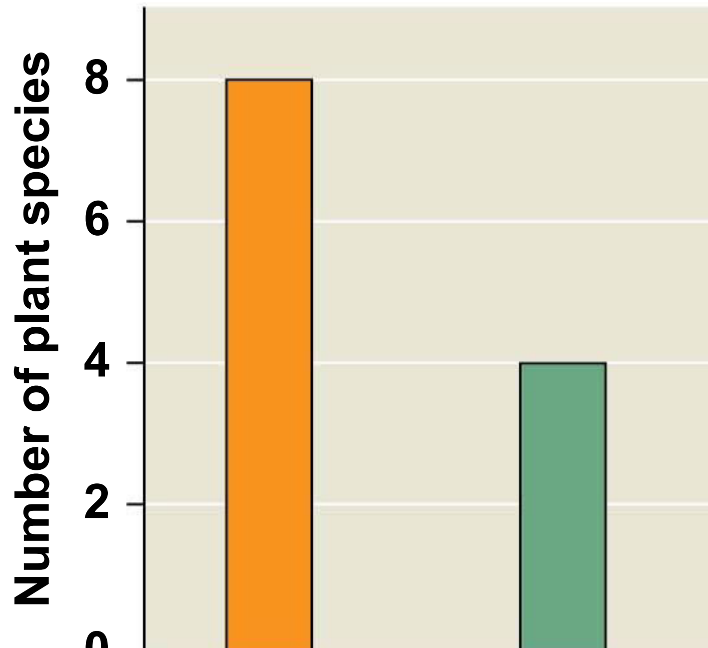
- The effects of ecological interactions can change
  - For example, cattle egrets typically have a commensal relationship with cattle, but occasionally the relationship is mutualistic

- Positive interactions have large effects on ecological communities
  - For example, the black rush, *Juncus gerardii*, makes the soil more hospitable for other plant species

Figure 41.9

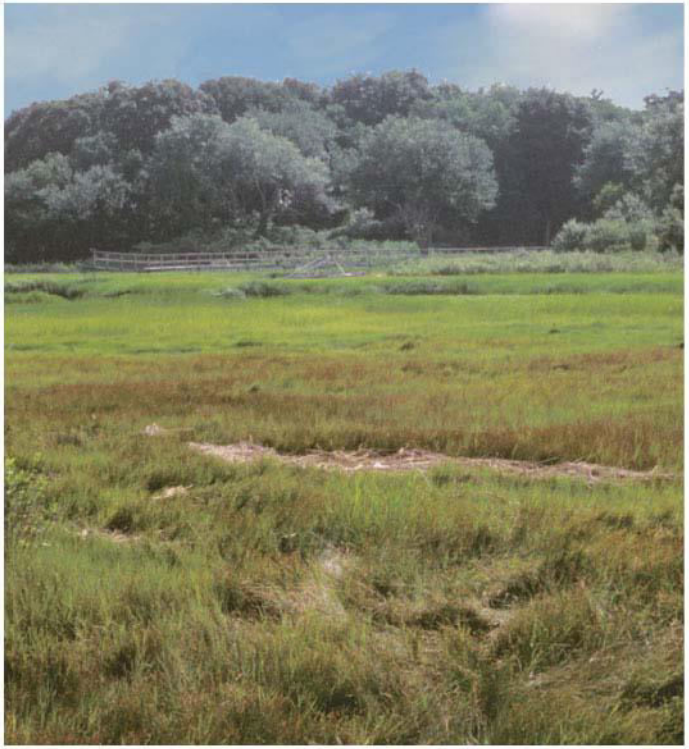


(a) Salt marsh with *Juncus* (foreground)



(b)

Figure 41.9-1



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

Concept 41.2: Diversity and trophic structure characterize biological communities

- Two fundamental features of community structure are species diversity and feeding relationships
- Sometimes a few species in a community exert strong control on that community's structure

Species Diversity

- **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 number of different species in the community
  - **Relative abundance** is the proportion each species represents of all individuals in the community

Figure 41.10

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

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

- Two communities can have the same species richness, but different relative abundances
- Diversity can be compared using a diversity index
  - Widely used is the **Shannon diversity index** (*H*)

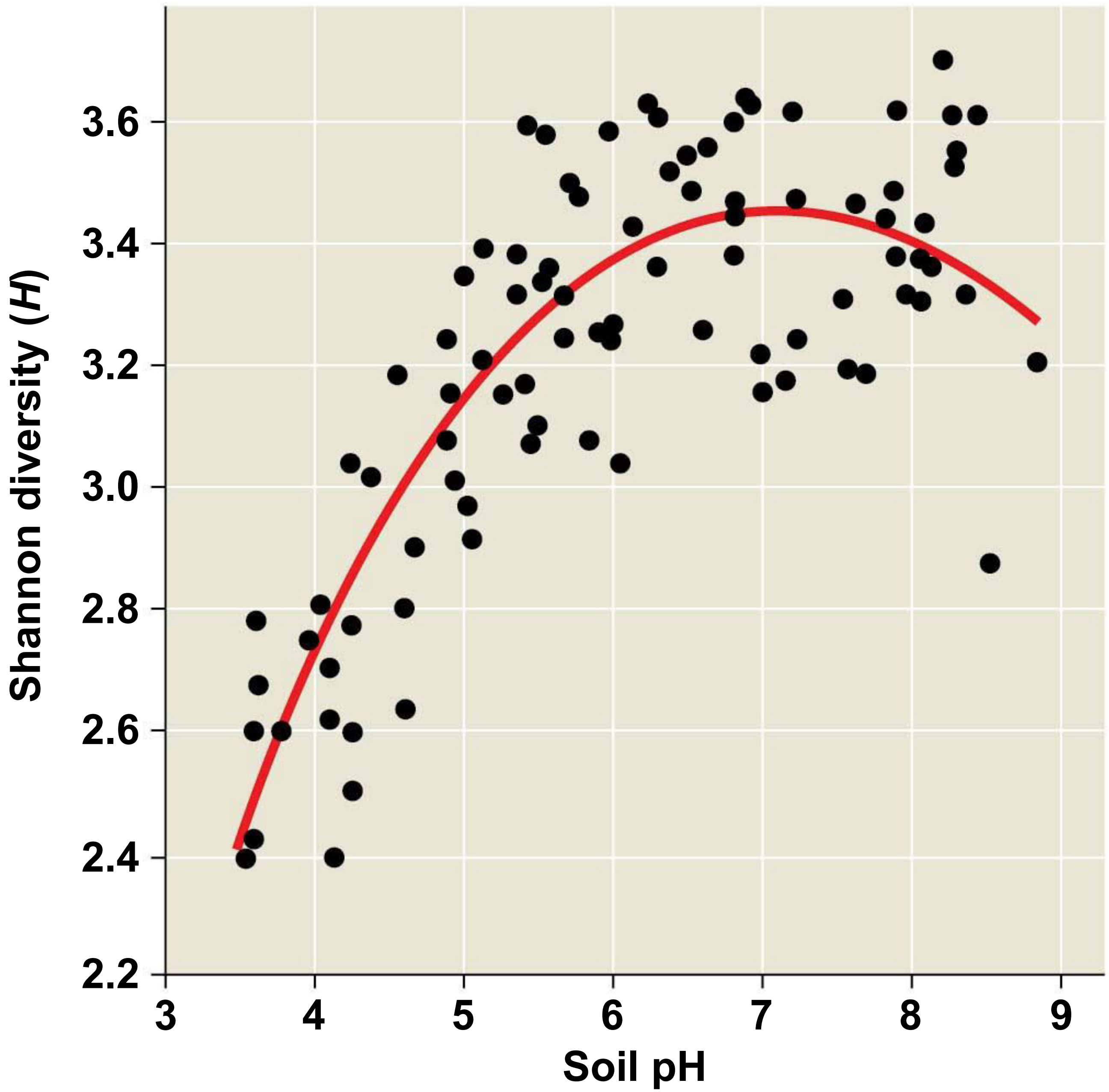
$$H = -(p_A \ln p_A + p_B \ln p_B + p_C \ln p_C + \ldots)$$

where A, B, C . . . are the species, *p* is the relative abundance of each species, and ln is the natural logarithm

- Determining the number and relative abundance of species in a community is challenging, especially for small organisms
- Molecular tools can be used to help determine microbial diversity

Figure 41.11

Results



Diversity and Community Stability

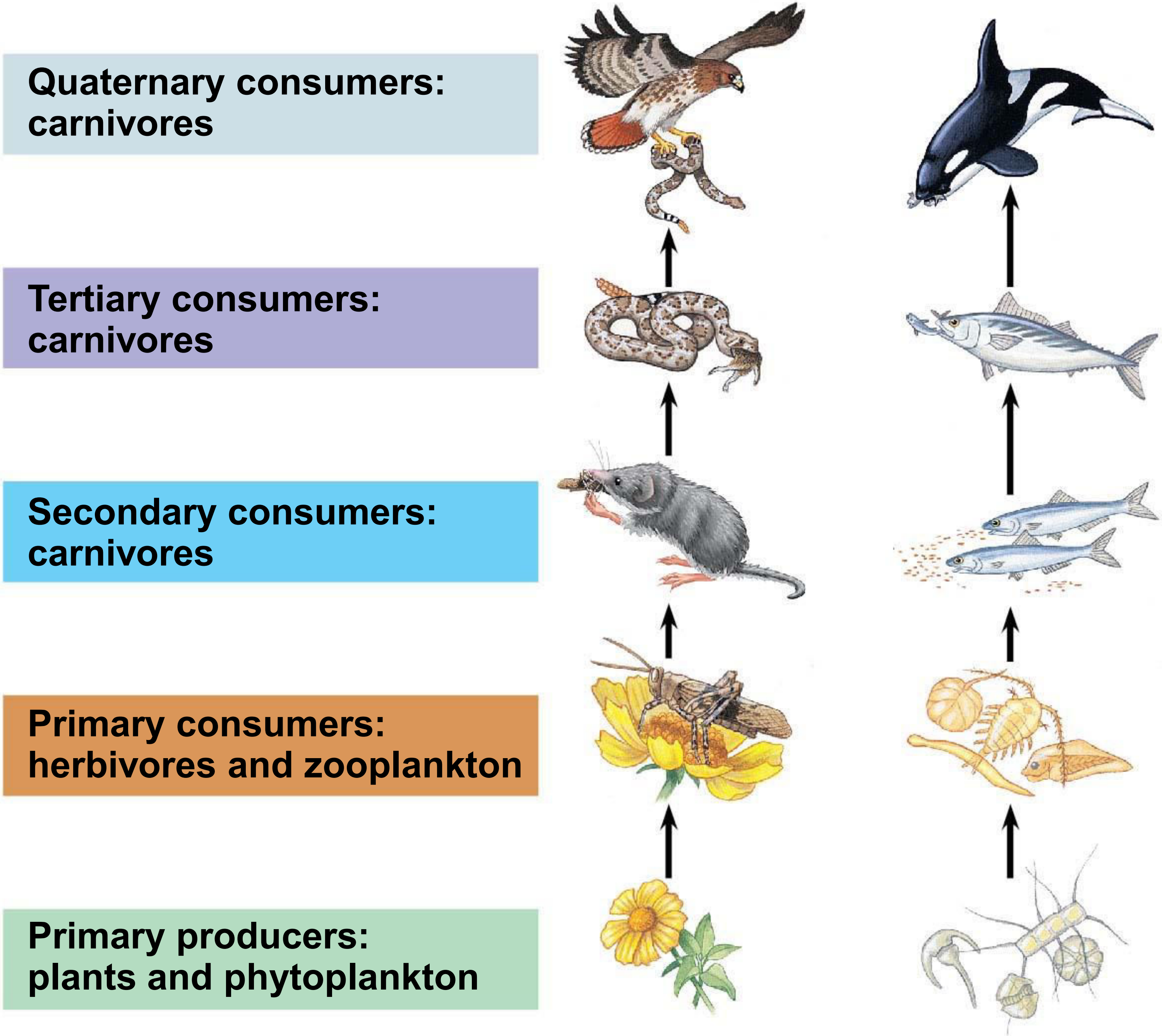
- Ecologists manipulate diversity in experimental communities to study the potential benefits of diversity
  - For example, plant diversity has been manipulated at Cedar Creek Ecosystem Science Reserve in Minnesota for two decades

- Results from the experiments at Cedar Creek indicate that communities with higher diversity are
  - More productive and more stable in their productivity
  - Better able to withstand and recover from environmental stresses
  - Able to produce more **biomass** (the total mass of all organisms in a habitat) than single-species communities
  - More resistant to **invasive species**, organisms that become established outside their native range

Trophic Structure

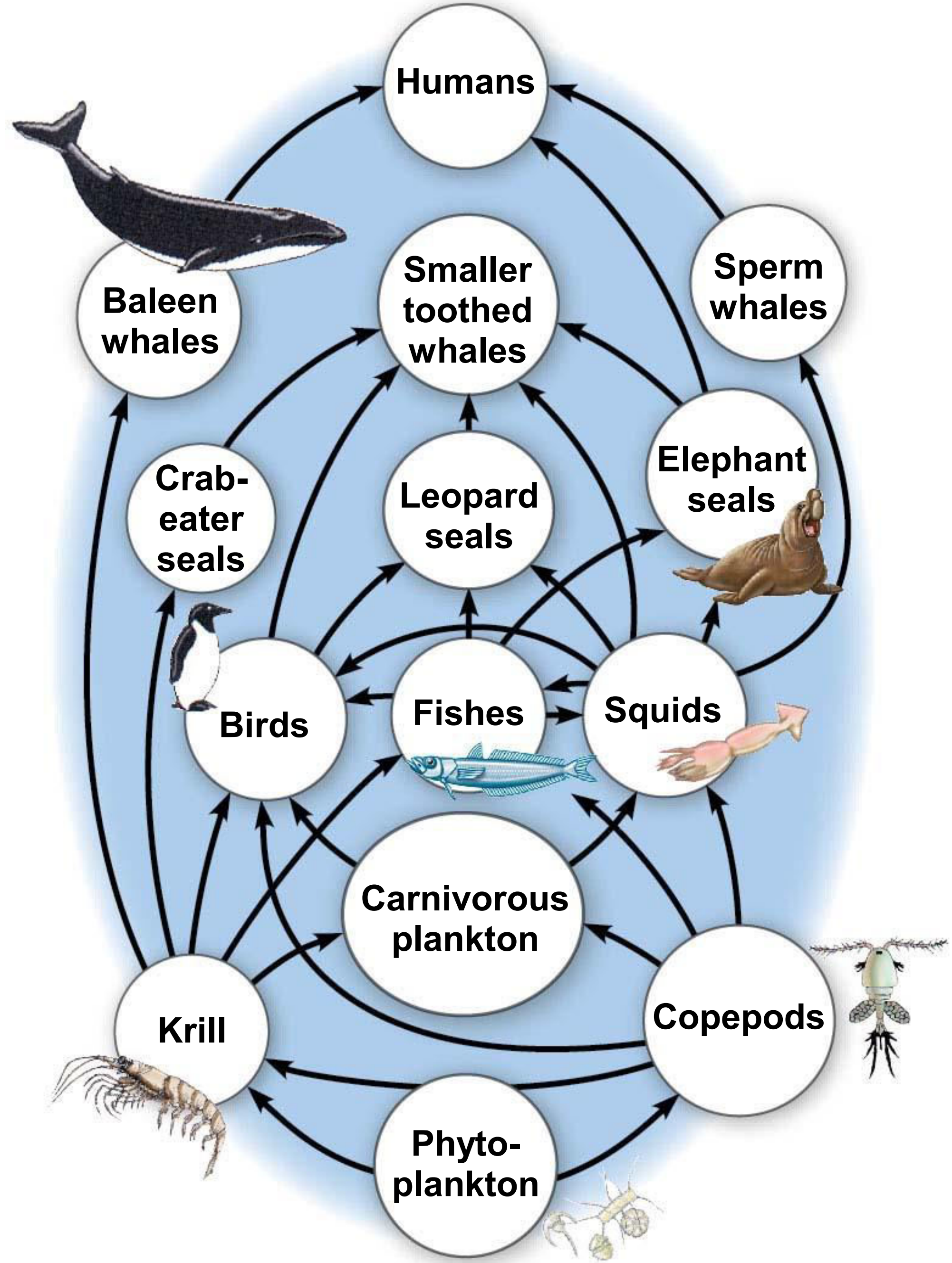
- **Trophic structure** refers to the feeding relationships between organisms in a community
- It is a key factor in community dynamics
- **Food chains** link trophic levels from producers to top carnivores

Figure 41.13


Quaternary consumers:
carnivores
Tertiary consumers:
carnivores
Secondary consumers:
carnivores
Primary consumers:
herbivores and zooplankton
Primary producers:
plants and phytoplankton

- A **food web** is a branching food chain with complex trophic interactions
- Species may play a role at more than one trophic level

Figure 41.14


Humans
Baleen whales
Smaller toothed whales
Sperm whales
Elephant seals
Crab-eater seals
Leopard seals
Birds
Fishes
Squids
Carnivorous plankton
Krill
Copepods
Phyto-plankton

Species with a Large Impact

- Certain species have a very large impact on community structure
- Such species are highly abundant or play a pivotal role in community dynamics

- **Dominant species** are those that are most abundant or have the highest biomass
- One hypothesis suggests that dominant species are most competitive in exploiting resources
- Another hypothesis is that they are most successful at avoiding predators and disease

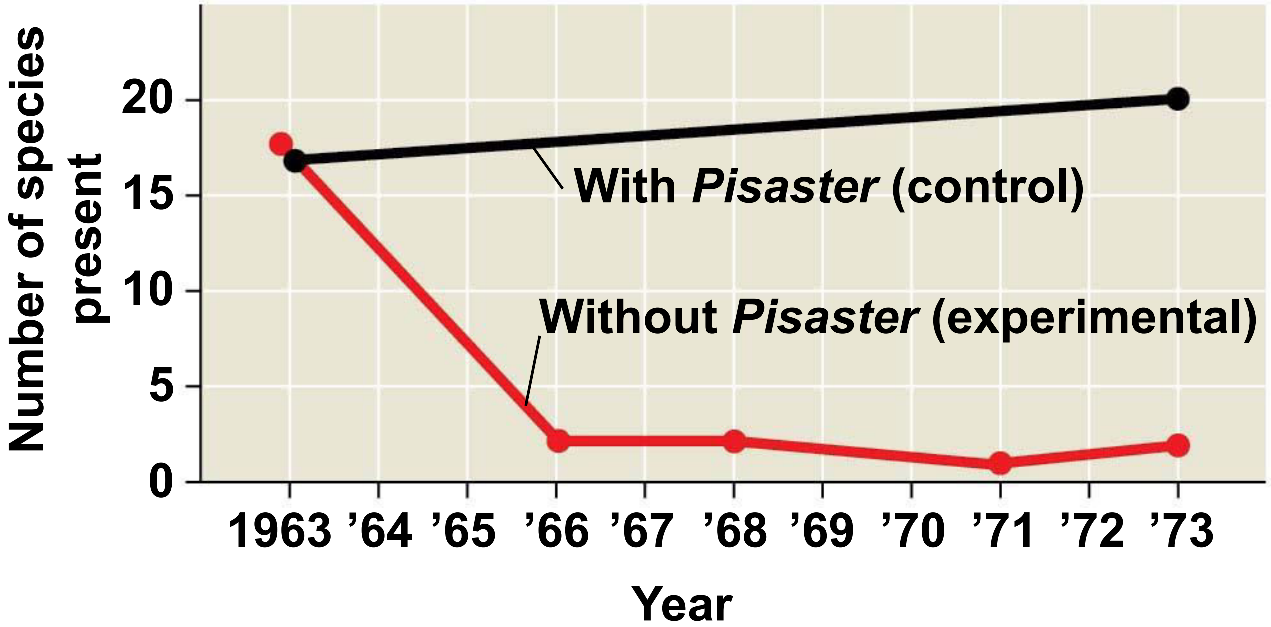
- **Keystone species** exert strong control on a community by their ecological roles, or niches
- In contrast to dominant species, they are not necessarily abundant in a community
- Field studies of sea stars illustrate their role as a keystone species in intertidal communities

Figure 41.15

Experiment

Pisaster ochraceus

Results



- **Ecosystem engineers** (or “foundation species”) cause physical changes in the environment that affect community structure
  - For example, beaver dams can transform landscapes on a very large scale

Bottom-Up and Top-Down Controls

- The **bottom-up model** of community organization proposes a unidirectional influence from lower to higher trophic levels
- In this case, the availability of mineral nutrients determines the abundance of primary producers
- The abundance of primary producers controls food availability and abundance for all higher trophic levels

- The bottom-up model can be represented by the equation

$$N \rightarrow V \rightarrow H \rightarrow P$$

where

N = mineral nutrients

V = plants

H = herbivores

P = predators

- The **top-down model**, also called the trophic cascade model, proposes that predation controls community organization
- In this case, predators control the abundance of herbivores, which in turn control primary producers

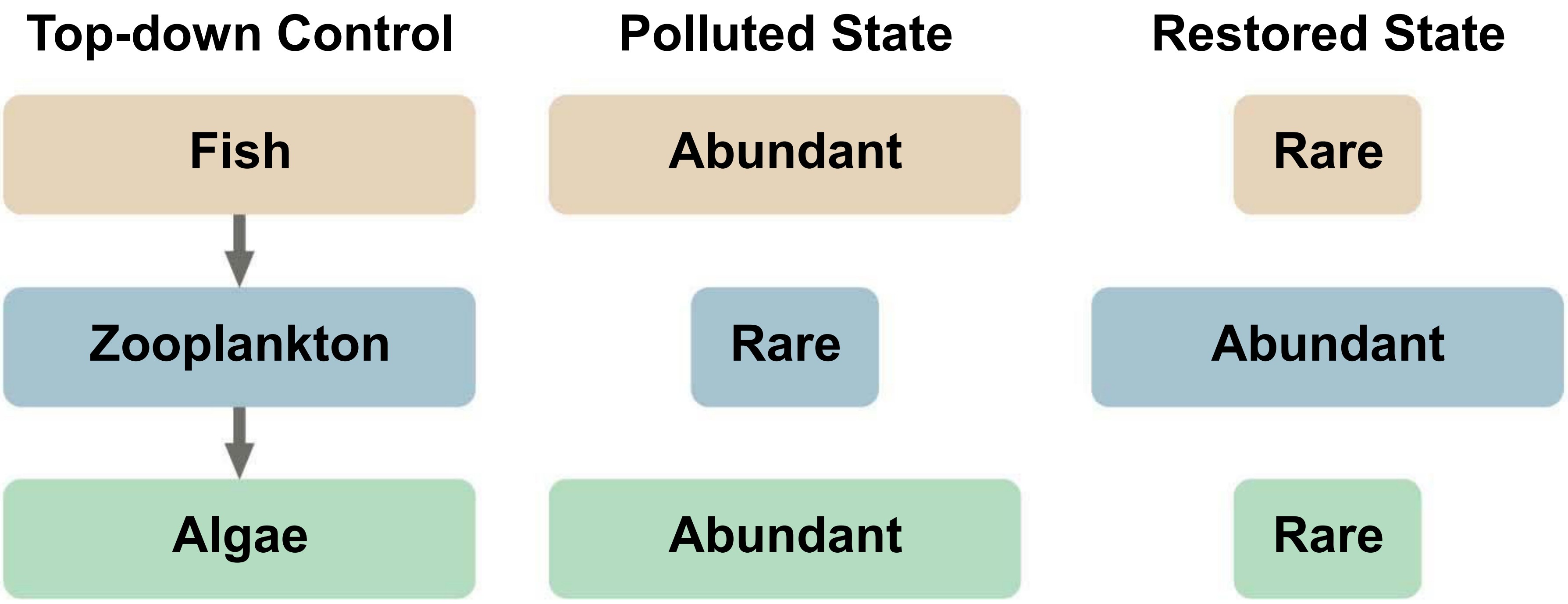
$$N \leftarrow V \leftarrow H \leftarrow P$$

- The effects move down the food chain as alternating +/– effects

- Ecologists can manipulate nutrient availability or top predator abundance and monitor changes in other trophic levels to understand how a community is organized

- **Biomanipulation** is an application of the top-down model used to improve water quality in polluted lakes
- Depending on the specific trophic structure of the lake, algae populations can be controlled by adding or removing top predators

Figure 41.17



Top-down Control
Polluted State
Restored State
Fish
Abundant
Rare
Zooplankton
Rare
Abundant
Algae
Abundant
Rare

Concept 41.3: Disturbance influences species diversity and composition

- Decades ago, most ecologists favored the view that communities are in a state of equilibrium
- The “balance of nature” view focused on interspecific competition as a key factor determining community composition and stability

- F. E. Clements argued that plant communities had only one stable equilibrium, a climax community controlled by climate
- A. G. Tansley argued that many potential stable communities were possible depending on a combination of environmental influences
- H. A. Gleason saw communities as chance assemblages of species with similar abiotic needs

- Some ecologists argued that disturbance could keep many communities from ever reaching equilibrium
- A **disturbance** is an event that changes a community by removing organisms or altering resource availability
- The **nonequilibrium model** describes communities as constantly changing after disturbances

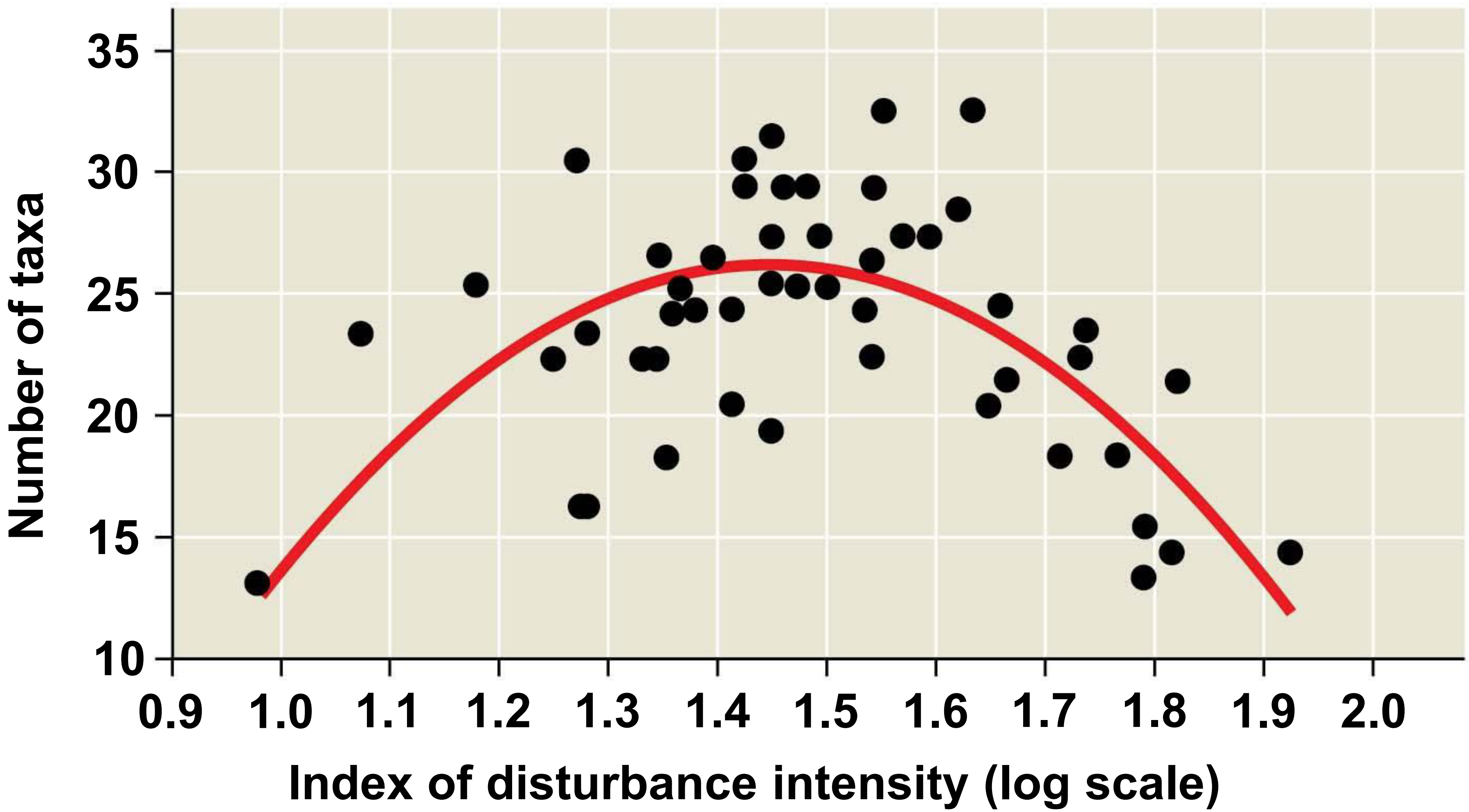
Characterizing Disturbance

- Storms, fires, floods, and drought are important sources of disturbance
- A high level of disturbance is often the result of a high intensity *and* high frequency of disturbance
- Low disturbance levels can result from either low intensity *or* low frequency of disturbance

- The **intermediate disturbance hypothesis** states that moderate levels of disturbance can foster greater diversity than either high or low levels of disturbance
- High levels of disturbance exclude many slow-growing or slow-colonizing species
- Low levels of disturbance allow dominant species to exclude less competitive species

- Intermediate levels of disturbance open up habitats for potential community members without severely altering conditions
  - For example, invertebrate diversity is highest in New Zealand stream beds when flooding frequency or intensity is intermediate

Figure 41.18


Number of taxa
35
30
25
20
15
10
0.9
1.0
1.1
1.2
1.3
1.4
1.5
1.6
1.7
1.8
1.9
2.0
Index of disturbance intensity (log scale)

- Small- and large-scale disturbances are a natural part of many communities
  - For example, the community in Yellowstone National Park recovers quickly even after large-scale fires
- The Yellowstone forest is an example of a nonequilibrium community

Figure 41.19

(a) Soon after fire

(b) One year after fire

Figure 41.19-1

(a) Soon after fire

Figure 41.19-2

(b) One year after fire

Ecological Succession

- **Ecological succession** is the sequence of change in community composition after a disturbance
- **Primary succession** occurs in nearly lifeless areas where there is no soil when succession begins
- **Secondary succession** begins in an area where soil remains after a disturbance

- Early-arriving species and later-arriving species may be linked in one of three processes
  - Early arrivals may facilitate the appearance of later species by making the environment favorable
  - Early species may inhibit the establishment of later species
  - Later species may tolerate conditions created by early species, but are neither helped nor hindered by them

- Retreating glaciers provide a valuable field research opportunity for observing succession
  - For example, succession on the moraines in Glacier Bay, Alaska, follows a predictable pattern of change in vegetation and soil characteristics

Figure 41.20-s1

Figure 41.20-s2

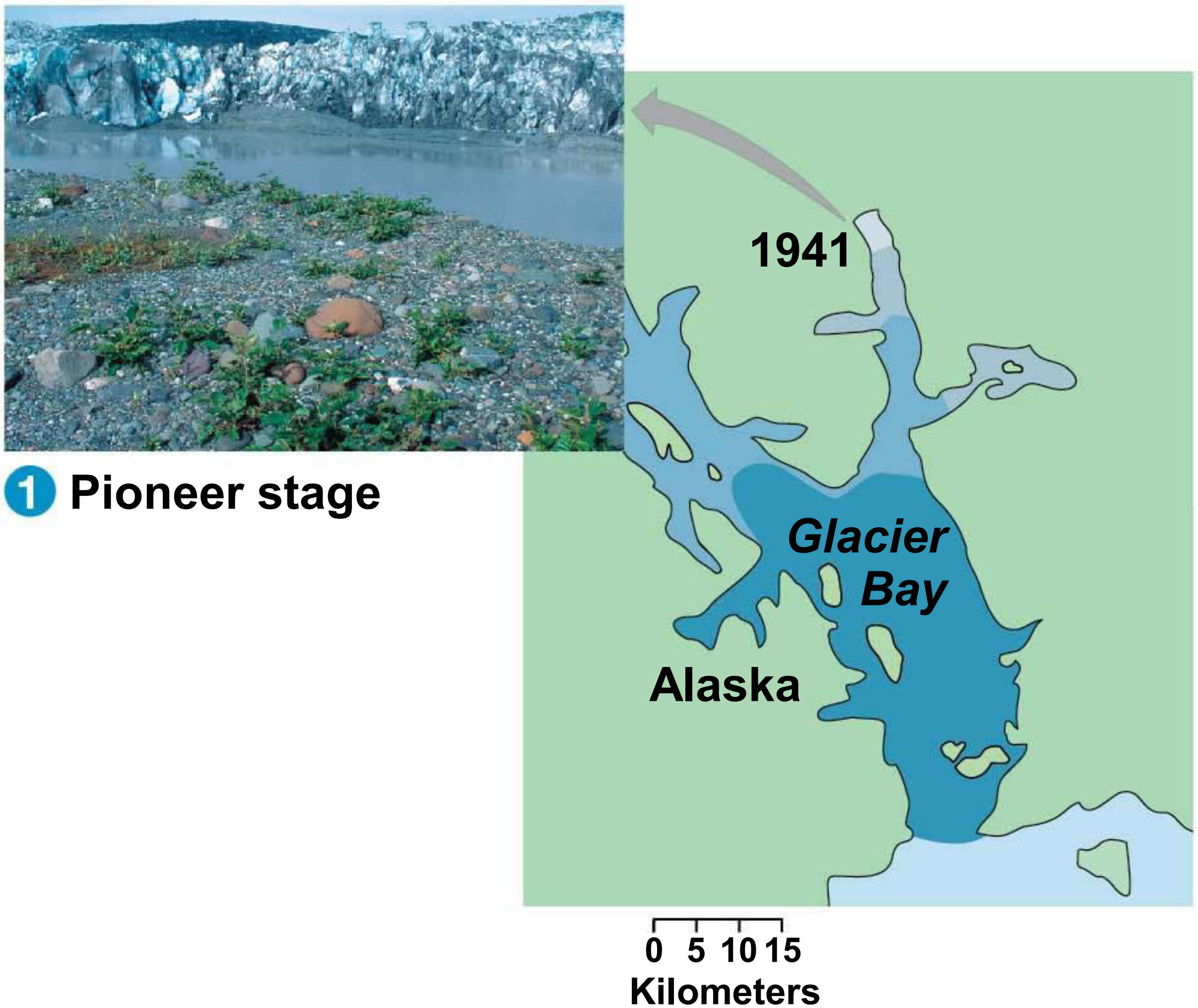


Figure 41.20-s3

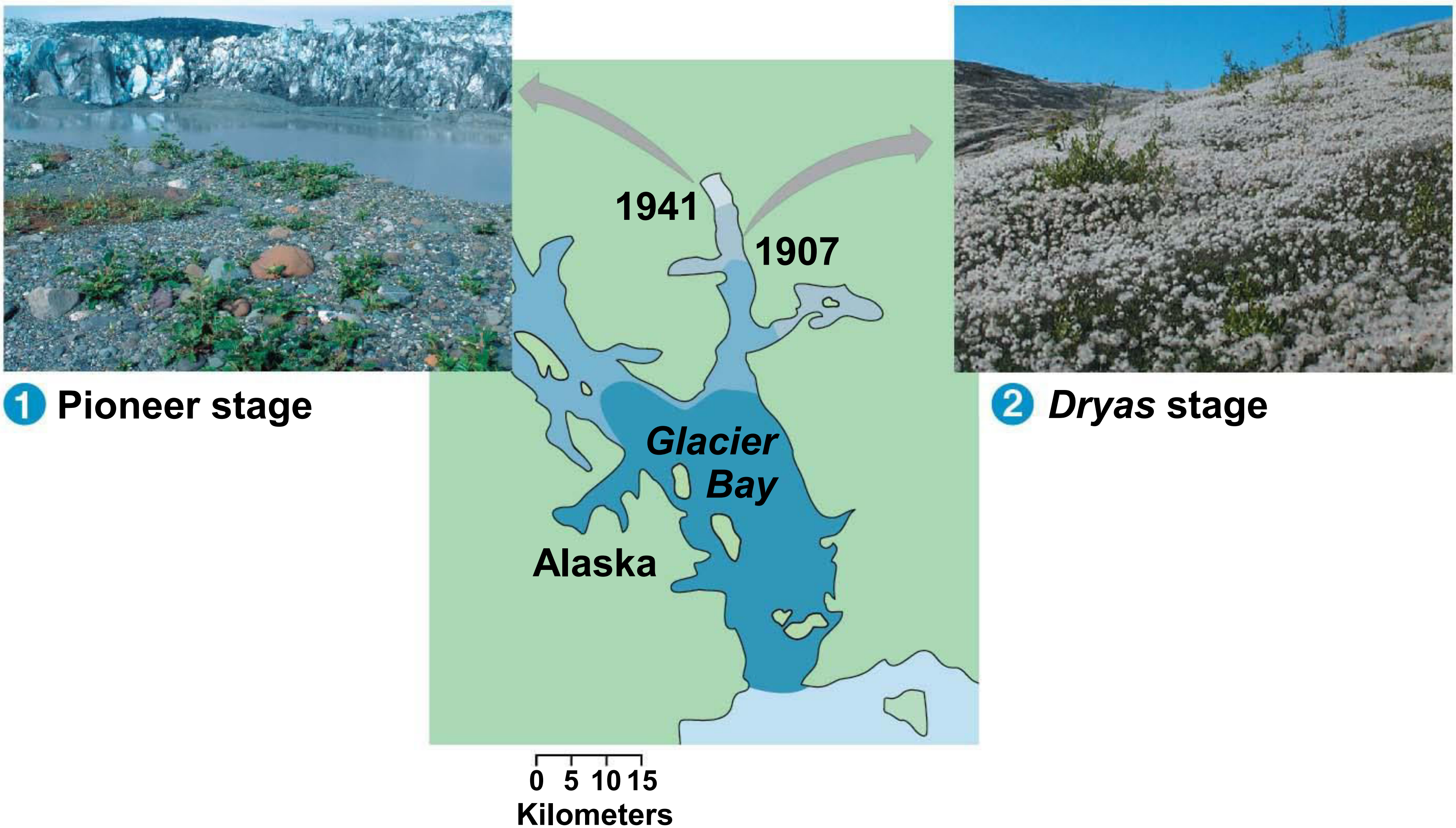


Figure 41.20-s4

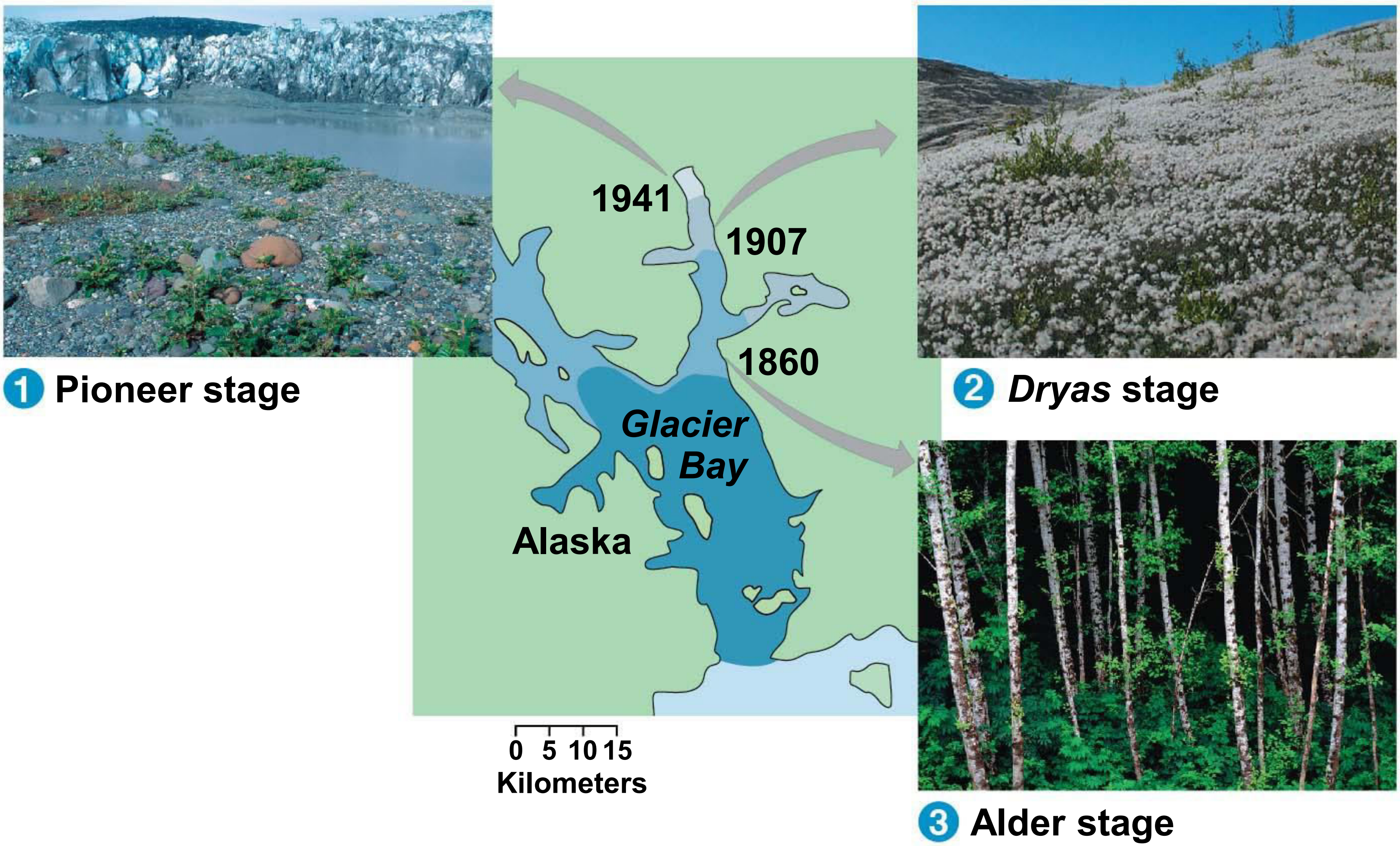
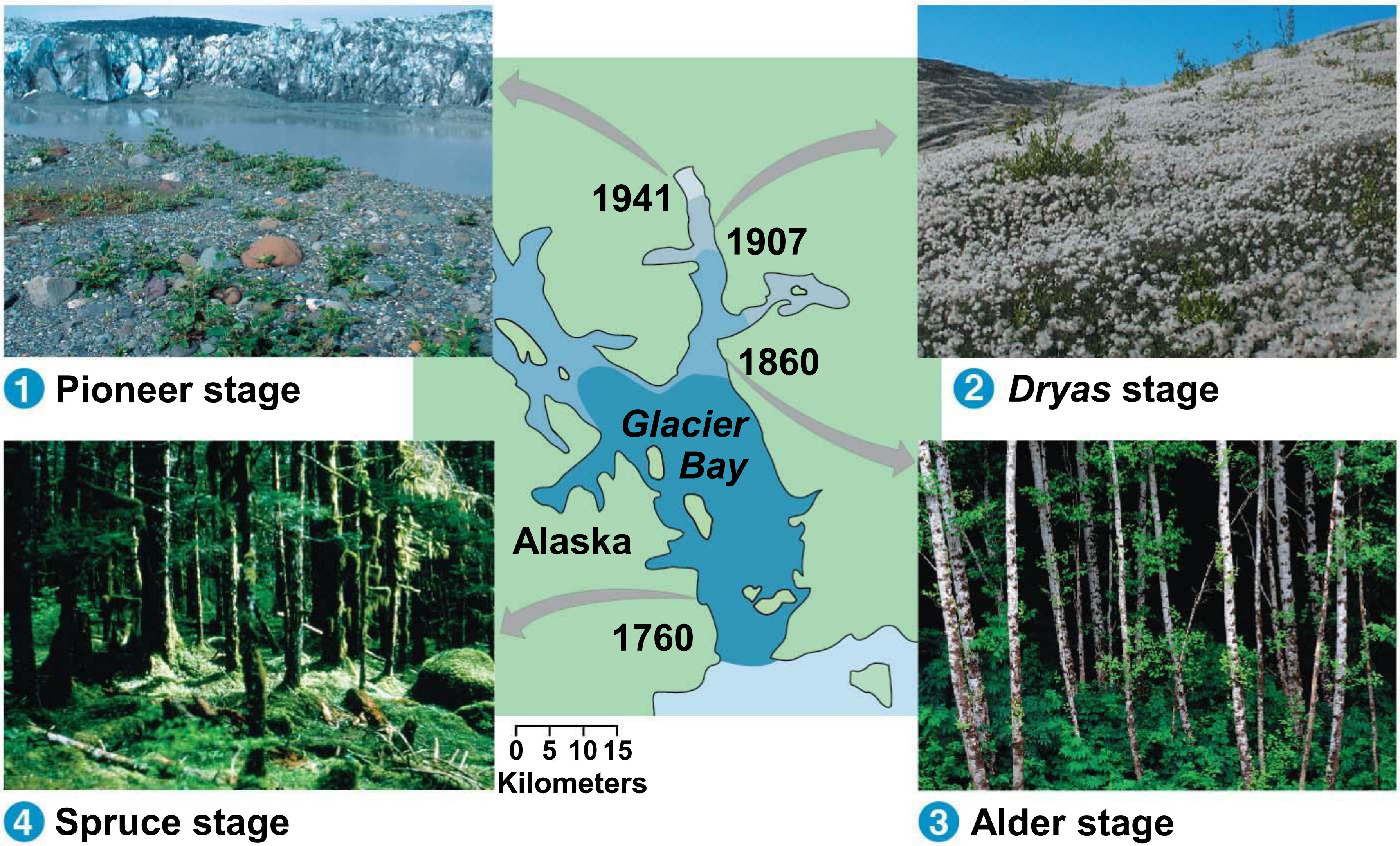


Figure 41.20-s5



1. The exposed moraine is colonized by pioneering plants, including liverworts, mosses, fireweed, *Dryas*, and willows

Figure 41.20-1

1 Pioneer stage

2. After about three decades, *Dryas* dominates the plant community

Figure 41.20-2

2 *Dryas* stage

3. A few decades later, alder invades and forms dense thickets

Figure 41.20-3

3 **Alder stage**

4. In the next two centuries, alder are overgrown by Sitka spruce, western hemlock, and mountain hemlock

- The forest is interspersed with sphagnum bogs, which form in areas of poor drainage

Figure 41.20-4

4 **Spruce stage**

- At Glacier Bay, succession is the result of changes induced by the vegetation itself; pioneer plant species facilitate colonization by later arriving species

Human Disturbance

- Human activities represent the strongest disturbances to ecosystems worldwide
- Examples include agricultural development, clear-cutting, overgrazing, and ocean trawling
- Human disturbance to communities usually reduces species diversity

Concept 41.4: Biogeographic factors affect community diversity

- Latitude and area are two key factors that affect a community's species diversity

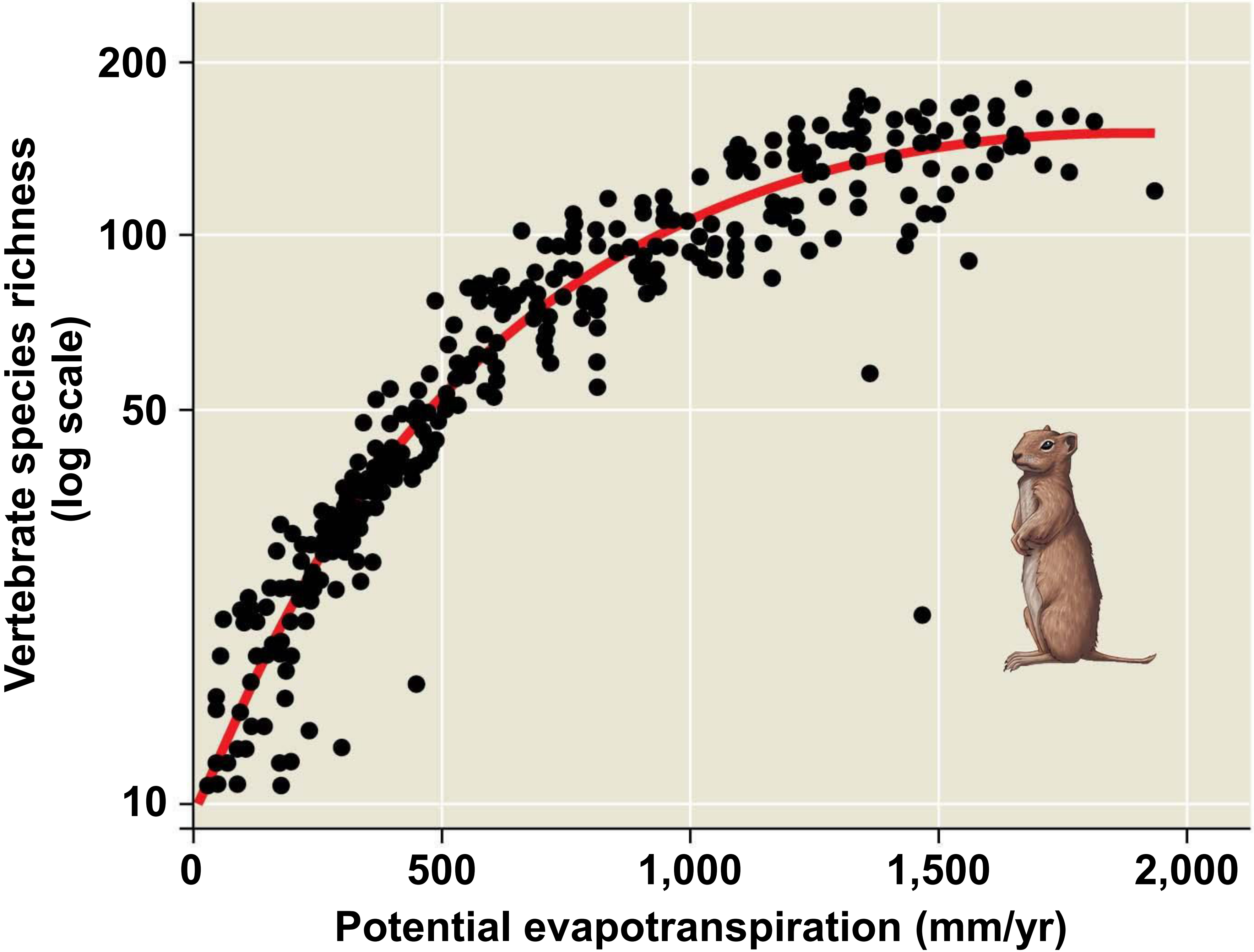
Latitudinal Gradients

- Species richness is greatest in the tropics and generally declines toward the poles
- Two key factors affecting latitudinal gradients are evolutionary history and climate

- Tropical communities are older and have had more time to accumulate new species through speciation
- Temperate and polar communities have had to “start over” repeatedly after major disturbances such as glaciations

- Climate is another key factor affecting latitudinal gradients in biodiversity
- The two main climatic factors correlated with diversity are sunlight and precipitation
- They 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

Figure 41.22


Vertebrate species richness
(log scale)
200
100
50
10
0
500
1,000
1,500
2,000
Potential evapotranspiration (mm/yr)

Area Effects

- The **species-area curve** quantifies the idea that, all other factors being equal, a larger geographic area has more species
- Islands are ideal for studying biogeographic factors affecting diversity

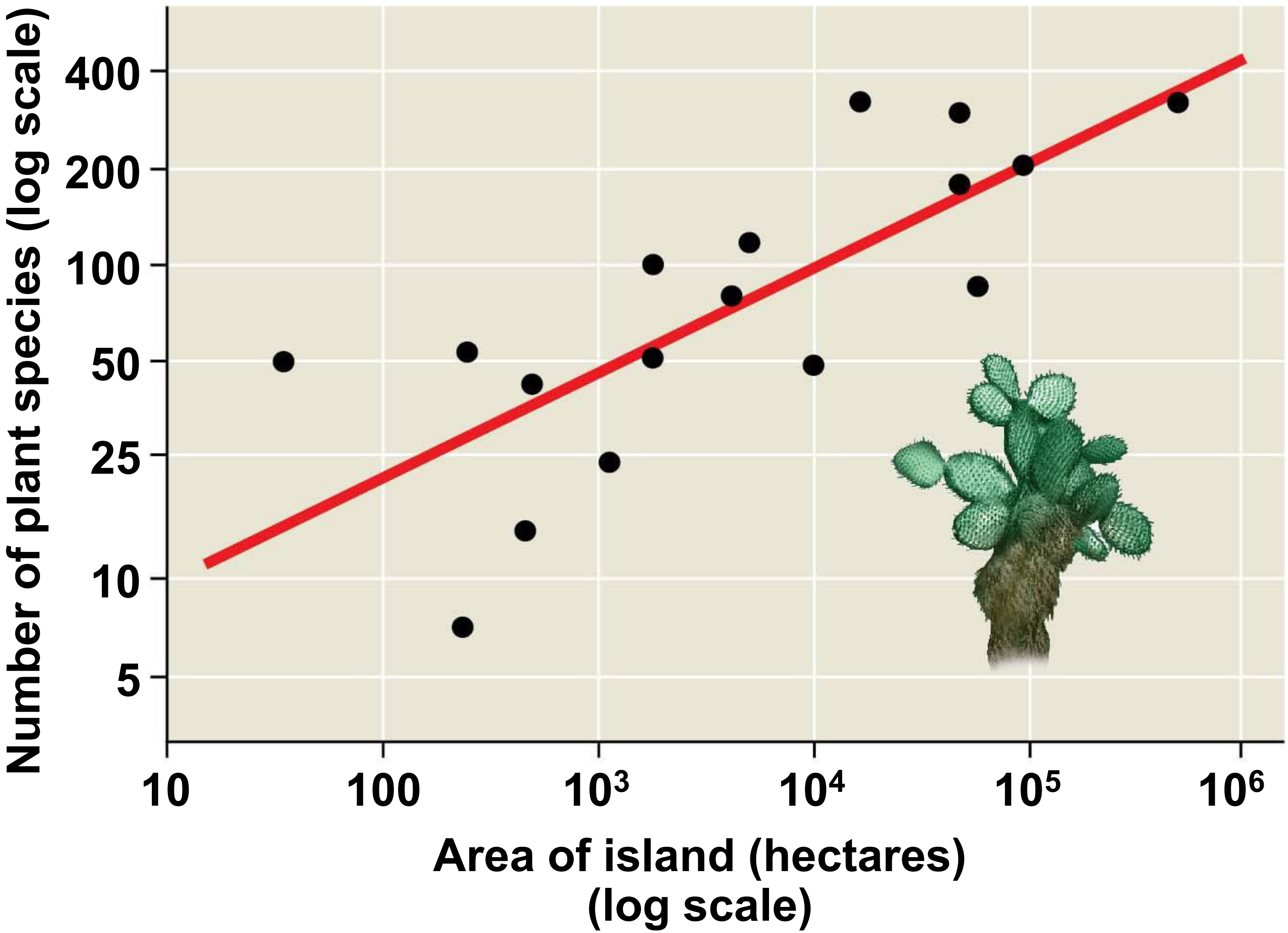
- Species richness on islands depends on rates of immigration and extinction
- These rates depend on island size; smaller islands have lower immigration rates and higher extinction rates
- They are also affected by distance from the mainland; closer islands receive more immigrants and have lower rates of extinction

- The island equilibrium model predicts species richness will reach a dynamic equilibrium where immigration is balanced by extinction
- The number of species at the equilibrium point is a function of island size and distance from mainland

- Studies of species richness on the Galápagos Islands support the prediction that species richness increases with island size

Figure 41.23

Results



Concept 41.5: Pathogens alter community structure locally and globally

- Ecological communities are universally affected by **pathogens**, disease-causing microorganisms and viruses

Effects on Community Structure

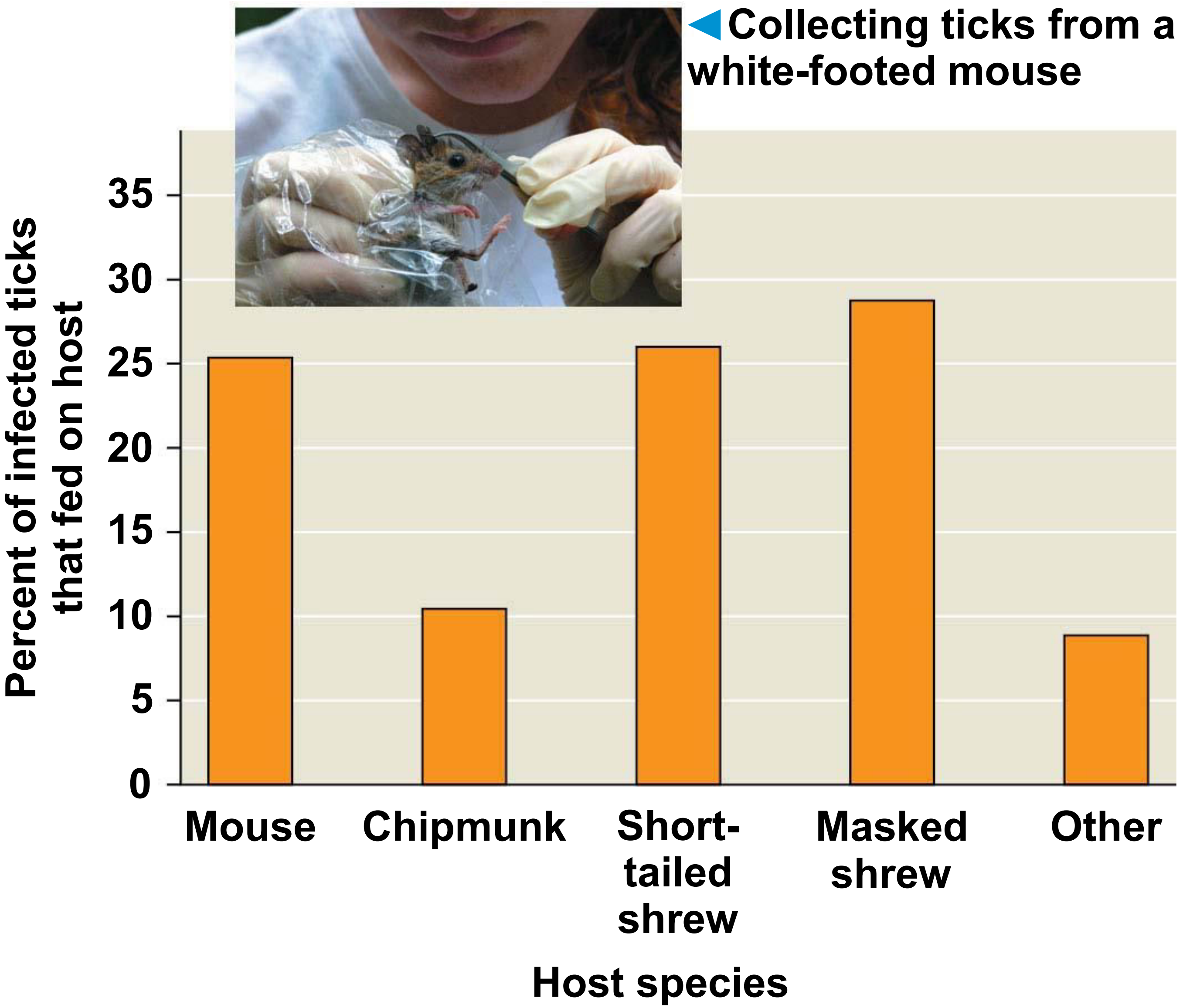
- Pathogens can have dramatic effects on community structure when they are introduced into new habitats
  - For example, coral reef communities are being decimated by white-band disease
  - Sudden oak death has killed millions of oaks that support many bird species

Community Ecology and Zoonotic Diseases

- **Zoonotic pathogens** are pathogens that have been transferred from other animals into humans
- The transfer of pathogens can be direct or through an intermediate species called a **vector**
- Many of today's emerging human diseases are zoonotic

- Identifying the community of hosts and vectors for a pathogen can help prevent disease
  - For example, recent studies identified two species of shrew as the primary hosts of the pathogen for Lyme disease

Figure 41.24


Collecting ticks from a white-footed mouse
Percent of infected ticks that fed on host
35
30
25
20
15
10
5
0
Mouse
Chipmunk
Short-tailed shrew
Masked shrew
Other
Host species

- Ecologists can use knowledge of community interactions to study the spread of zoonotic diseases
  - For example, ecologists are tracking the spread of avian flu in human and domestic and wild bird host populations

- Human activities are transporting pathogens around the world at unprecedented rates
- Community ecology is needed to help study and combat pathogens

Figure 41.UN01-1

Type of Prey Offered	Percentage of Snakes from Each Area That Ate the Native Frog vs. Cane Toad	
	Area with Cane Toads Present for 40–60 Years	Area with No Cane Toads
Native frog	100	100
Cane toad	0	50

Figure 41.UN01-2

Number of Years Cane Toads Were Present in the Area	5	10	10	20	50	60	60	60	60	60
Percent Reduction in Snake Swimming Speed	52	19	30	30	5	5	9	11	12	22

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

Figure 41.UN03

Interaction	Description
Competition (–/–)	Two or more species compete for a resource that is in short supply.
Exploitation (+/–)	One species benefits by feeding upon the other species, which is harmed. Exploitation includes:
Predation	One species, the predator, kills and eats the other, the prey.
Herbivory	An herbivore eats part of a plant or alga.
Parasitism	The parasite derives its nourishment from a second organism, its host, which is harmed.
Positive interactions (+/+ or +/0)	One species benefits, while the other species benefits or is not harmed. Positive interactions include:
Mutualism (+/+)	Both species benefit from the interaction.
Commensalism (+/0)	One species benefits, while the other is not affected.