

11

Competition



11 Competition

- *Case Study*: Competition in Plants that Eat Animals
- Competition for Resources
- General Features of Competition
- Competitive Exclusion
- Altering the Outcome of Competition
- *Case Study Revisited*
- *Connections in Nature*: The Paradox of Diversity

Case Study: Competition in Plants that Eat Animals

Charles Darwin was the first to provide clear evidence of carnivory in plants.

Plants use a variety of mechanisms to eat animals.

The Venus flytrap has modified leaves that attract insects with nectar. The inner surface has touch-sensitive hairs; if an insect trips those hairs, the leaf snaps shut in half a second.

Figure 11.1 A Plant that Eats Animals



Case Study: Competition in Plants that Eat Animals

Pitcher plants lure insects into a pitcher-shaped trap.

The inside of the pitcher has downward-facing hairs, which make it easy for the insect to crawl in, but hard to crawl out.

About halfway down, many pitchers have a layer of wax that sticks to the insect's feet, causing it to tumble into a vat that contains water or digestive juices.

Case Study: Competition in Plants that Eat Animals

Why do some plants eat animals?

Competition among plants can be intense where soil nutrients are scarce.

In nutrient-poor environments, carnivory in plants has evolved multiple times.

Carnivory may be an adaptation to low-nutrient environments, to avoid competing with other plants.

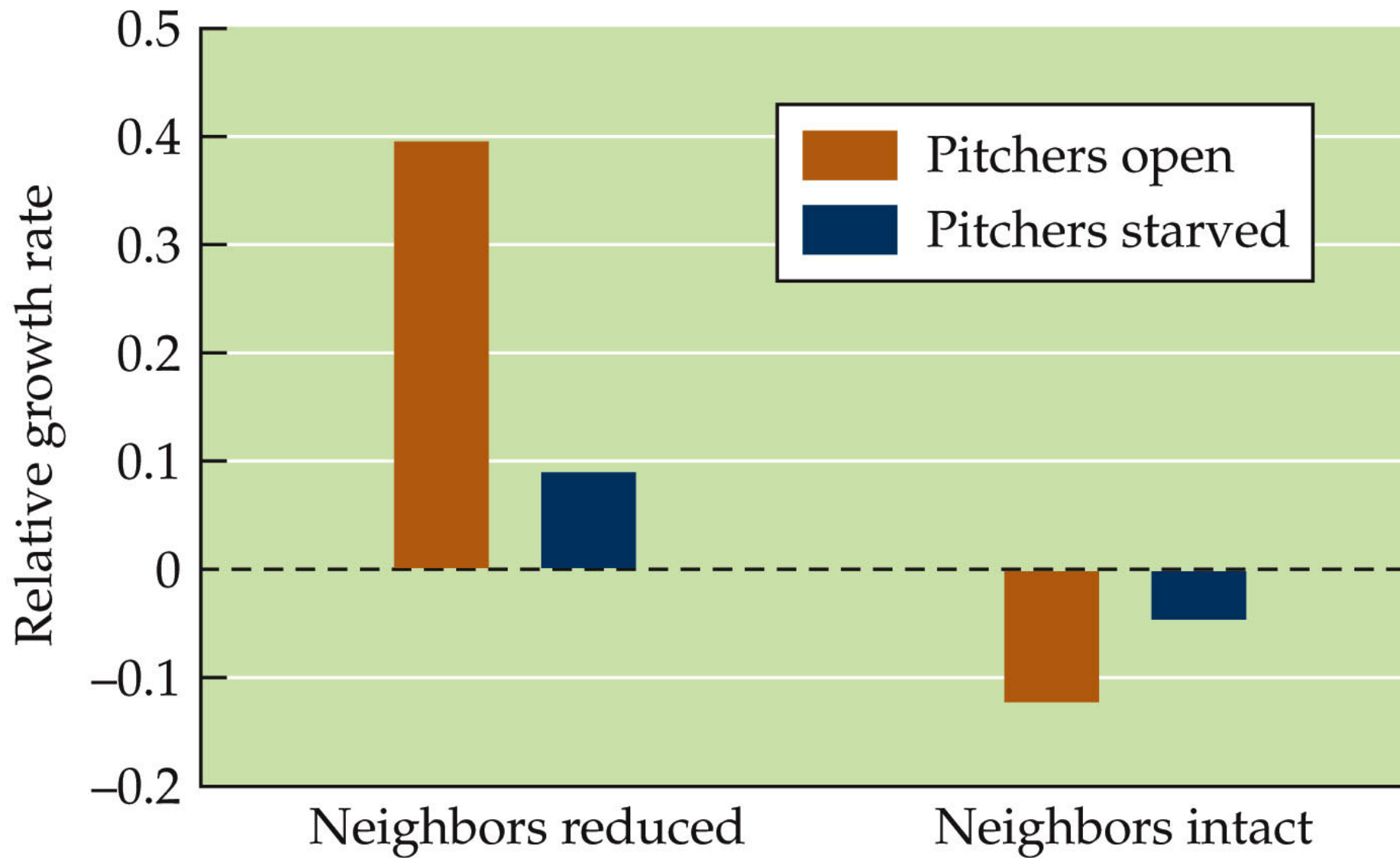
Case Study: Competition in Plants that Eat Animals

In experiments with pitcher plants *Sarracenia alata*, Brewer (2003) removed noncarnivorous competitor plants. Some pitcher plants were also deprived of prey (starved).

Growth rates increased when competitors were removed.

But with neighbors intact, and pitchers covered, the growth rate was not reduced as expected.

Figure 11.2 Competition Decreases Growth in a Carnivorous Plant



Introduction

A. G. Tansley did one of the first experiments on competition in 1917.

He wanted to explain the distribution of two species of bedstraw: *Galium hercynicum*, which was restricted to acidic soils, and *G. pumilum*, restricted to calcareous soils.

Introduction

Tansley found that if grown alone, each species could survive on both acidic and calcareous soils.

But when grown together, soil type determined which would survive.

Tansley inferred that competition restricted the two species to particular soil types in nature.

Interspecific competition is an interaction between two species in which each is harmed when they both use the same limiting resource.

Intraspecific competition can occur between individuals of a single species.

Competition for Resources

Concept 11.1: Competition occurs between species that share the use of a resource that limits the growth, survival, or reproduction of each species.

Organisms compete for **resources**—features of the environment that are required for growth, survival, or reproduction, and which can be consumed to the point of depletion.

Competition for Resources

Examples of resources that can be consumed to depletion:

- Food.
- Water in terrestrial habitats.
- Light for plants.
- Space, especially for sessile organisms.
- For mobile animals, space for refuge, nesting, etc.

Figure 11.3 Space Can Be a Limiting Resource



Competition for Resources

Species are also influenced by factors that are not consumed, such as temperature, pH, salinity.

These factors are not considered to be resources.

Physical factors affect population growth rates but are not consumed or depleted.

Competition for Resources

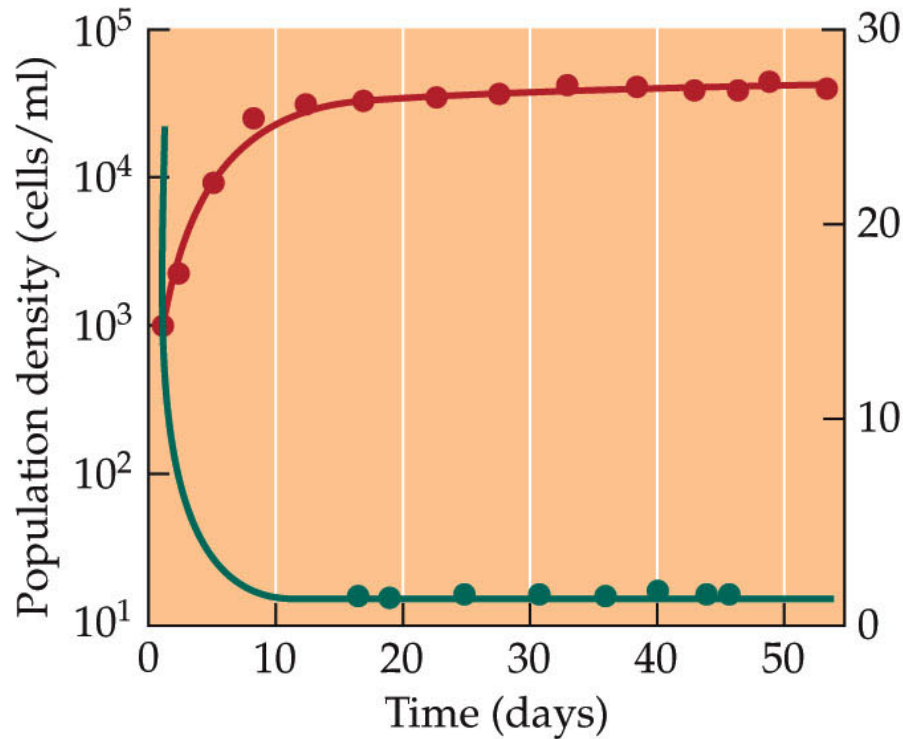
Experiments using two species of diatoms (single-celled algae that make cell walls of silica, SiO_2) were done by Tilman et al. (1981).

When each species was grown alone, a stable population size was reached and silica concentrations were reduced.

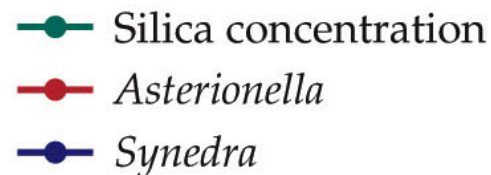
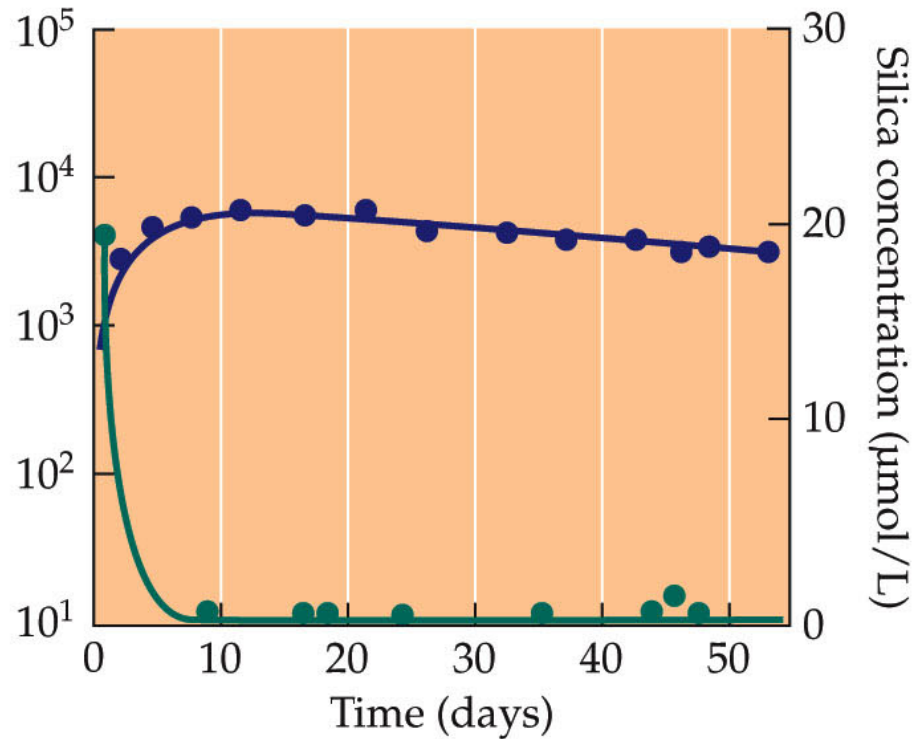
When grown together, the two species competed for silica, and one species drove the other to extinction.

Figure 11.4 Competing Organisms Can Deplete Resources (Part 1)

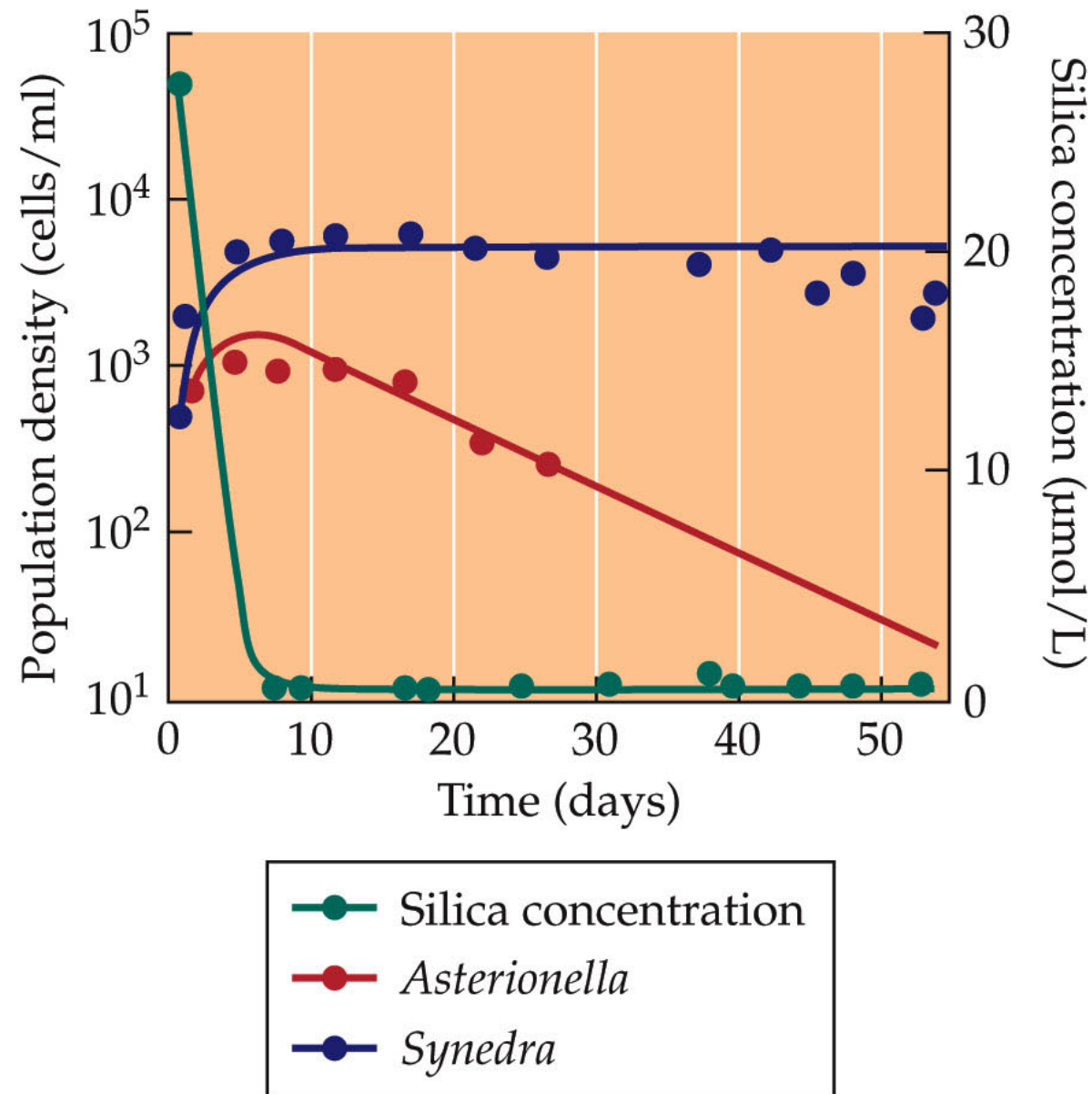
(A) *Asterionella* alone



(B) *Synedra* alone



(C) Interspecific competition



Competition for Resources

Competition should increase in intensity when resources are scarce.

Competition in plants might be expected to increase in importance when they are growing in nutrient-poor soils.

Using a perennial grass species, Wilson and Tilman (1993) were able to demonstrate this.

Competition for Resources

The grass species was transplanted into plots that had been growing with and without nitrogen fertilizer added.

Each plot type had 3 treatments:

1. Neighbors left intact.
2. Neighbor roots left intact but neighbor shoots tied back.
3. Neighbor roots and shoots both removed.

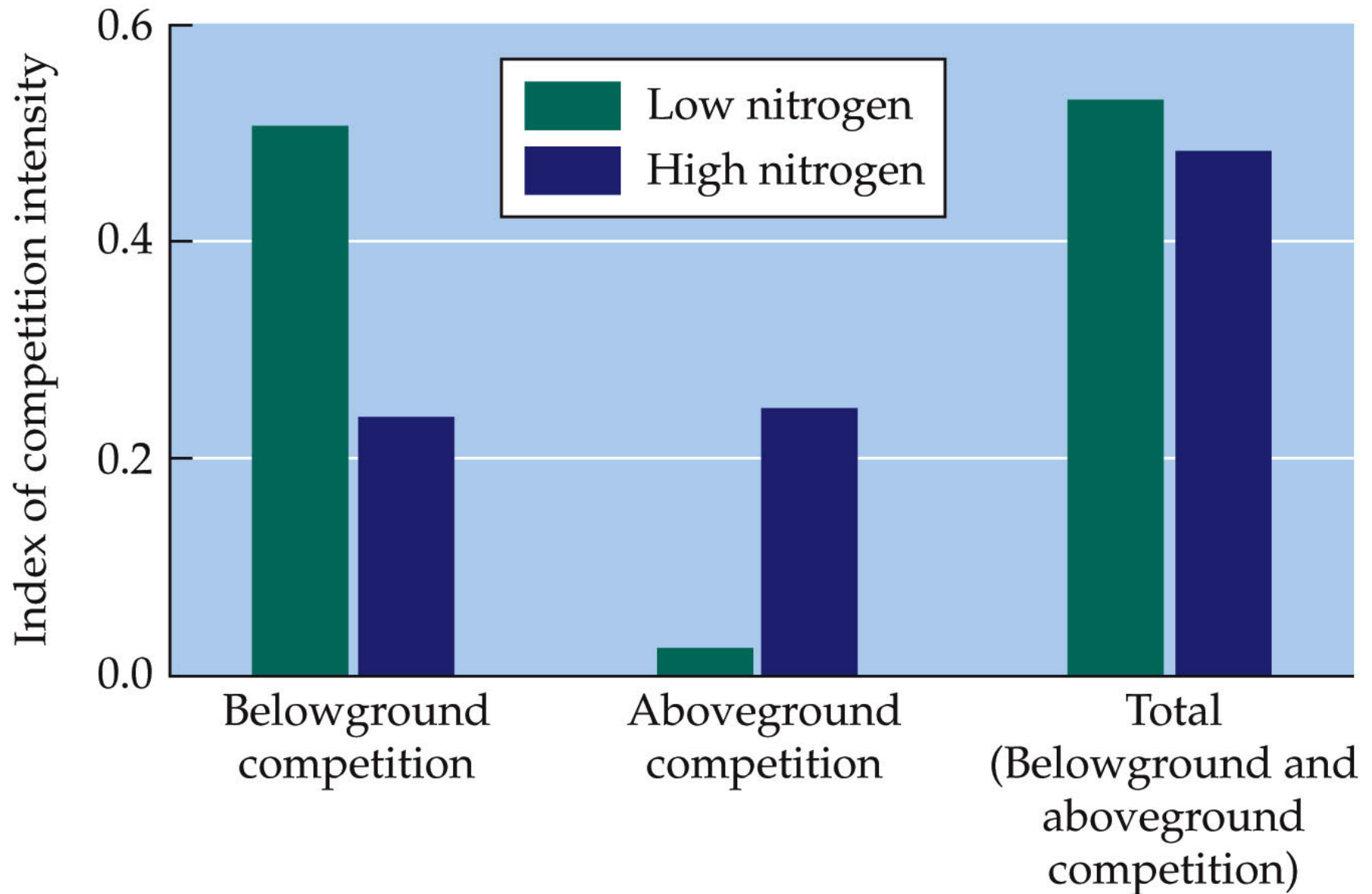
Competition for Resources

Treatment 1 would include both aboveground and belowground competition, which did not differ between the two plot types.

Belowground competition (treatment 2) was most intense in the nitrogen-limited plots.

Figure 11.5 A Resource Availability Affects the Intensity of Competition

(A)



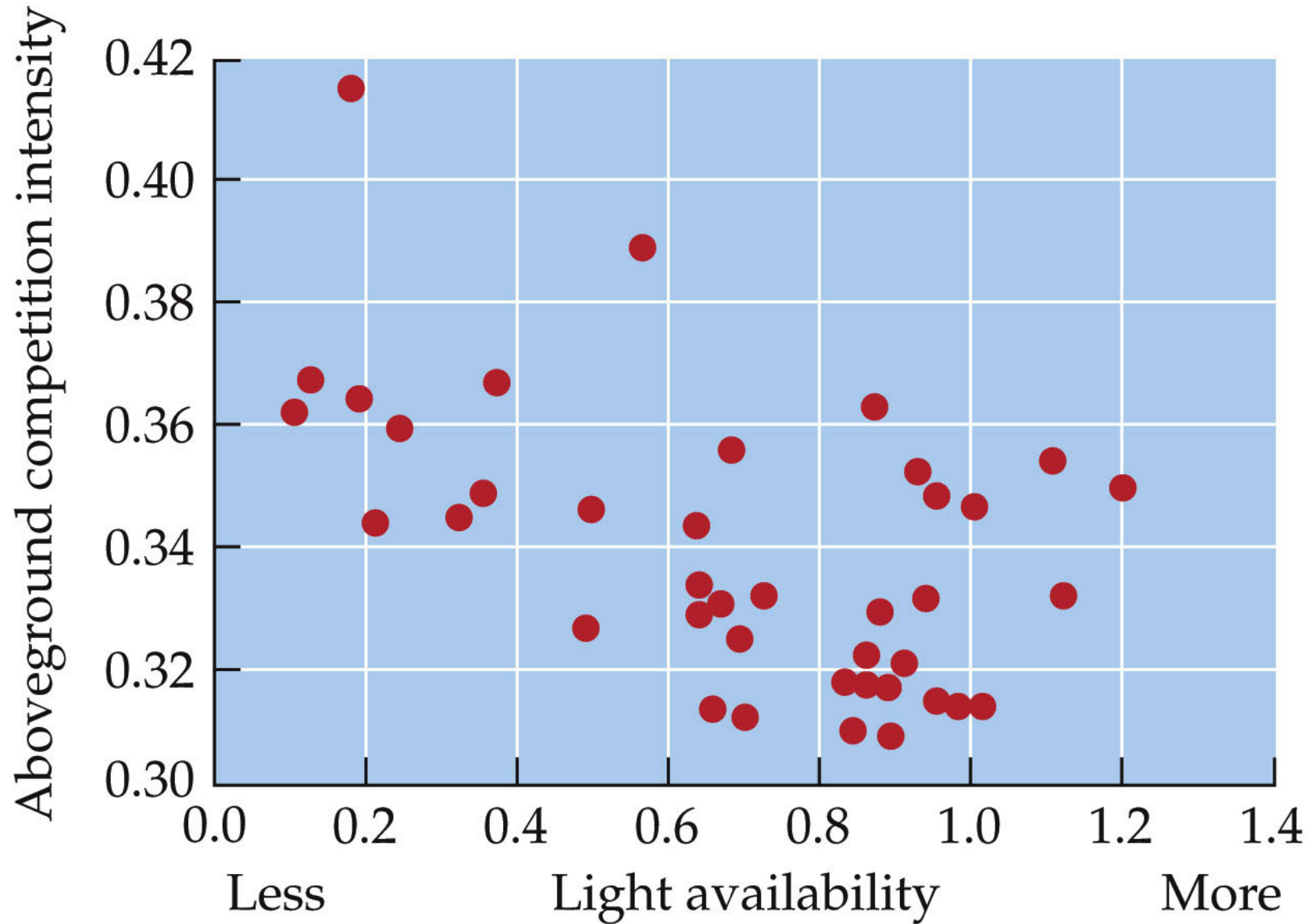
Competition for Resources

Aboveground competition was estimated by subtracting competition in treatment 2 from competition in treatment 1.

Aboveground competition for light increased when light levels were low.

Figure 11.5 B Resource Availability Affects the Intensity of Competition

(B)



Competition for Resources

How important is competition in ecological communities?

Results from many studies have been compiled and analyzed to answer this question.

Schoener (1983) found that of 390 species studied, 76% showed effects of competition under some conditions; 57% showed effects under all conditions tested.

Competition for Resources

Connell (1983) found that competition was important for 50% of 215 species in 72 studies.

Gurevitch et al. (1992) analyzed the magnitude of competitive effects found for 93 species in 46 studies. They showed that competition had significant effects on a wide range of organisms.

Competition for Resources

Potential biases in these analyses include failure of researchers to publish studies that show no significant effects, and a tendency for investigators to study species they suspect will show competition.

Still, they document that competition is common, though not ubiquitous.

General Features of Competition

Concept 11.2: Competition, whether direct or indirect, can limit the distributions and abundances of competing species.

As far back as Darwin, competition between species has been seen as an influence on evolution and species distributions.

General Features of Competition

Exploitation competition: Species compete indirectly through their mutual effects on the availability of a shared resource.

Competition occurs simply because individuals reduce the availability of a resource as they use it.

Examples: The pitcher plants and the diatoms

General Features of Competition

Interference competition: Species compete directly for access to a resource.

Individuals may perform antagonistic actions (e.g., when two predators fight over a prey item, or voles aggressively exclude other voles from preferred habitat).

General Features of Competition

Interference competition can also occur in sessile species.

Example: The acorn barnacle often crushes or smothers nearby individuals of another barnacle species as it grows. As a result, it directly prevents the other species from living in most portions of a rocky intertidal zone.

General Features of Competition

Allelopathy: A form of interference competition in which individuals of one species release toxins that harm other species.

Spotted knapweed, an invasive plant in North America, has been very successful and caused great economic damage to rangeland.

General Features of Competition

Cattle do not eat spotted knapweed, giving it an edge over native plants that cattle do eat.

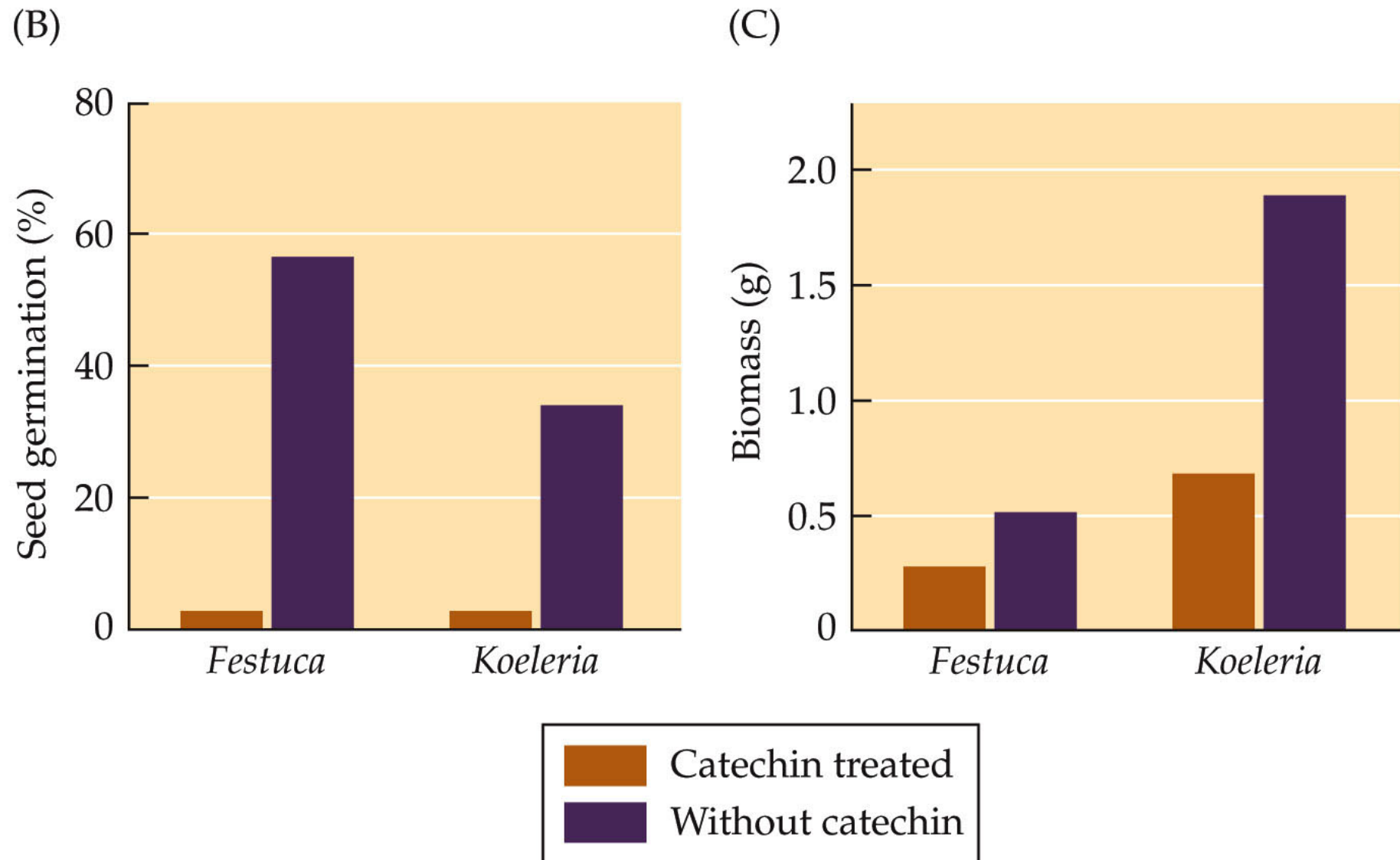
It also releases a toxin called catechin into surrounding soils, which has been shown to reduce germination and growth of native grasses.

Figure 11.6 Chemical Warfare in Plants (Part 1)

(A)



Figure 11.6 Chemical Warfare in Plants (Part 2)



General Features of Competition

For a resource in short supply, competition will reduce the amount available to each species.

In many cases the effects of competition are unequal, or asymmetrical, and one species is harmed more than the other.

Example: When one species drives another to extinction.

General Features of Competition

Competition can also occur between distantly related species.

In experiments with rodents and ants that eat the same seeds, Brown and Davidson (1977) set up plots with four treatments:

General Features of Competition

1. Wire mesh fence excluded seed-eating rodents.
2. Seed-eating ants were excluded by applying insecticides.
3. Both rodents and ants were excluded.
4. Undisturbed control plots.

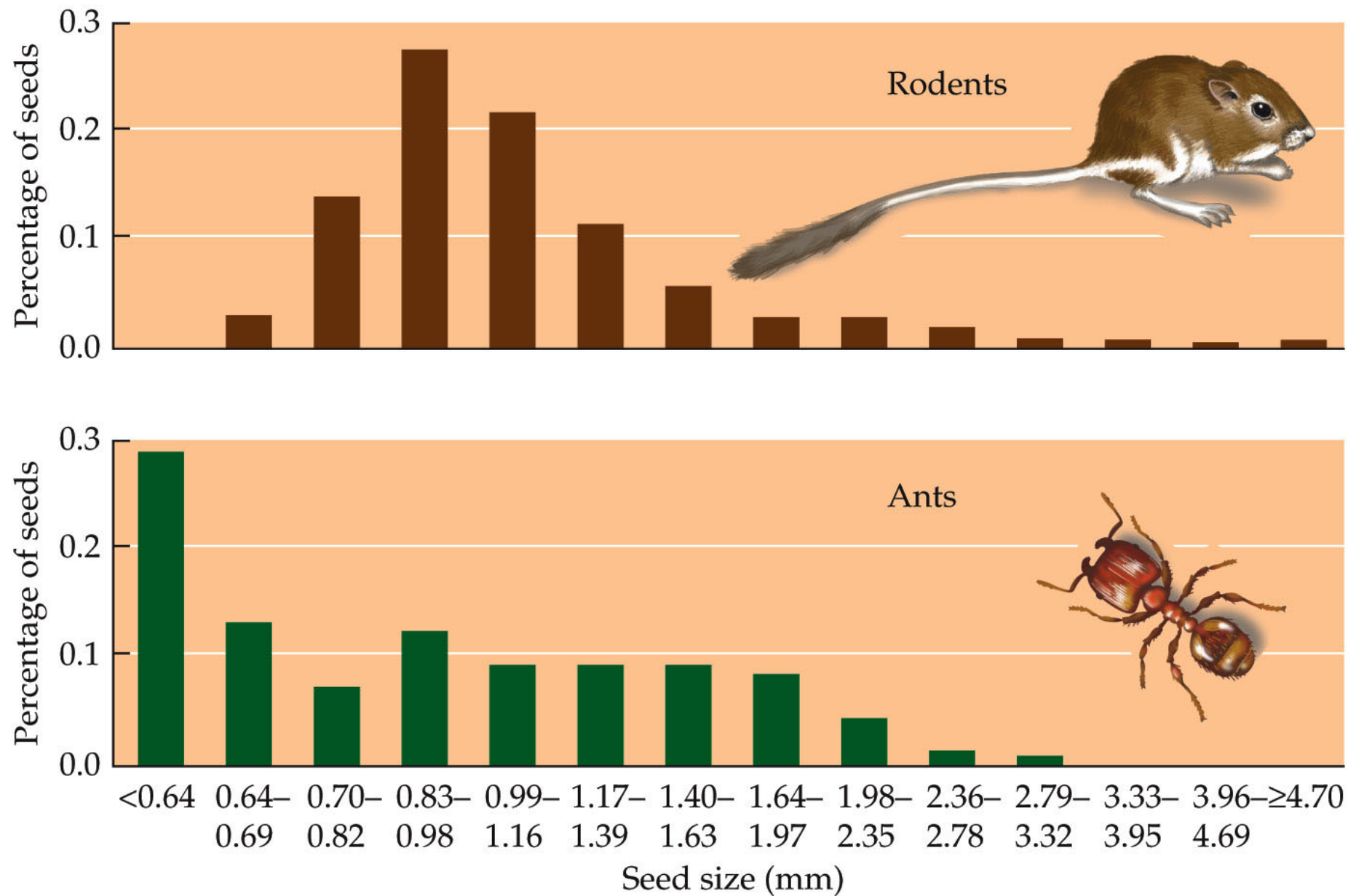
General Features of Competition

Where rodents were excluded, ant colonies increased by 71%.

Where ants were excluded, rodents increased in both number and biomass.

Where both were excluded, the number of seeds increased by 450%.

Figure 11.7 Ants and Rodents Compete for Seeds



General Features of Competition

When either rodents or ants were removed, the group that remained ate roughly as many seeds as rodents and ants combined ate in the control plots.

In natural conditions, each group would be expected to eat fewer seeds in the presence of the other group than it could eat when alone.

General Features of Competition

Competition can also limit distribution and abundance of species.

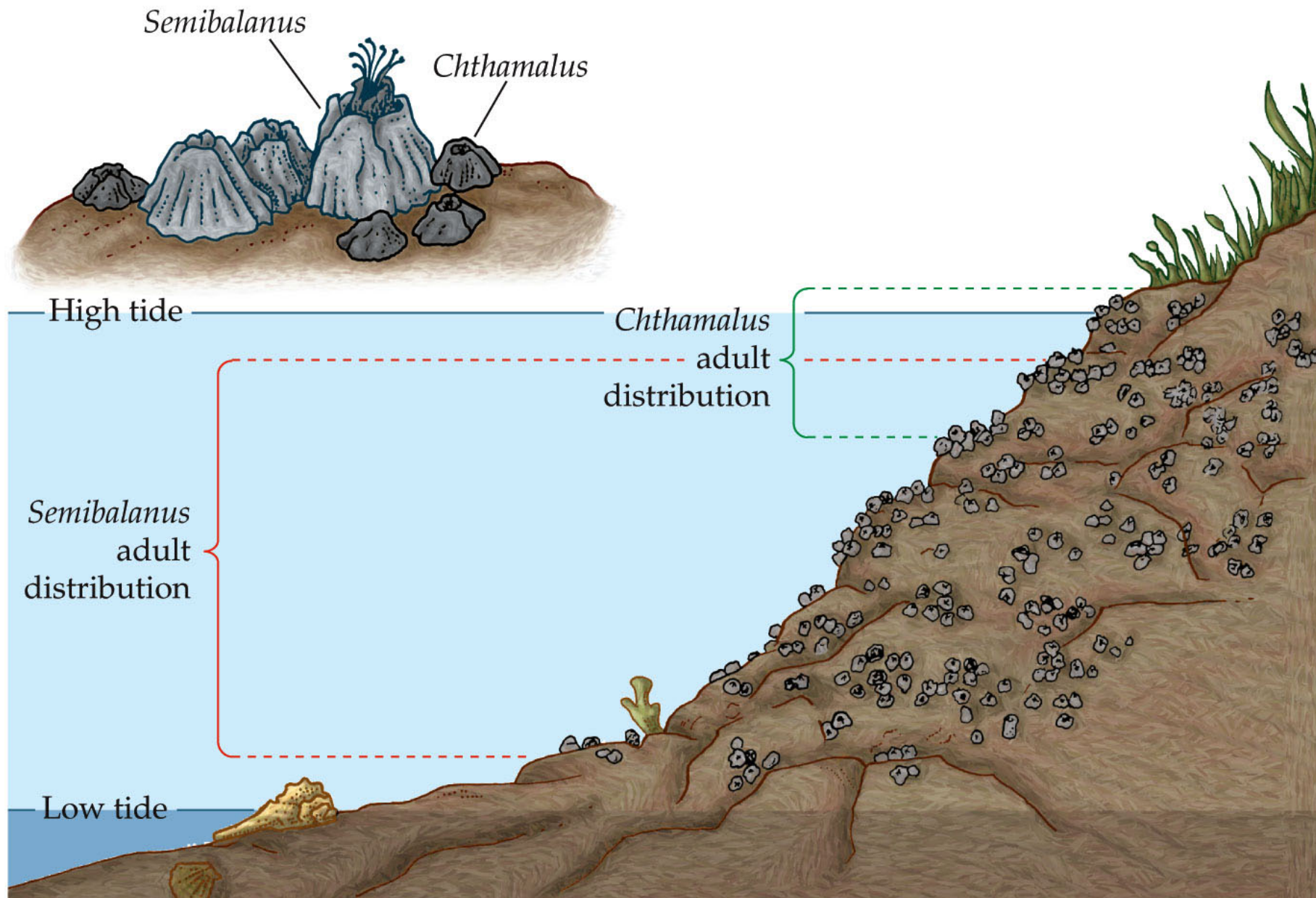
Connell (1961) examined factors that influenced the distribution, survival, and reproduction of two barnacle species, *Chthamalus stellatus* and *Semibalanus balanoides*, on the coast of Scotland.

General Features of Competition

Distribution of larvae of the two species overlapped throughout the upper and middle intertidal zones.

Adult distributions did not overlap:
Chthamalus were found only near the top of the intertidal zone; adult *Semibalanus* were found throughout the rest of the intertidal zone.

Figure 11.8 Squeezed Out by Competition



General Features of Competition

Using removal experiments, Connell found that competition with *Semibalanus* excluded *Chthamalus* from all but the top of the intertidal zone.

Semibalanus smothered, removed, or crushed the other species.

However, *Semibalanus* dried out and survived poorly at the top of the intertidal zone.

General Features of Competition

Competition can also affect geographic distribution.

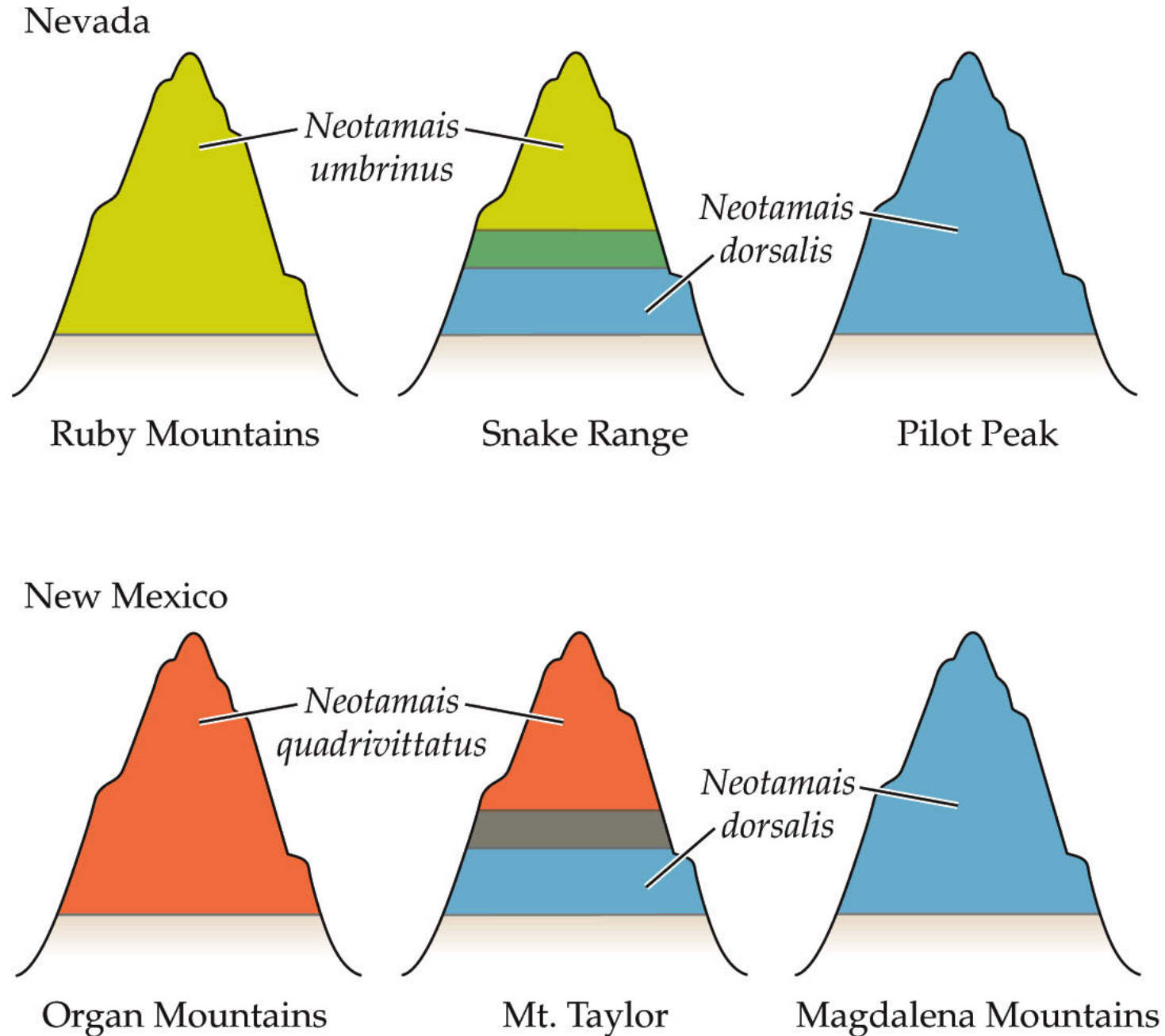
A natural experiment refers to a situation in nature that is similar in effect to a controlled removal experiment.

General Features of Competition

Chipmunk species in the southwestern U.S. live in mountain forests.

Patterson (1980, 1981) found that when a chipmunk species lived alone on a mountain range, it occupied a broader range of habitats and elevations than when it lived with a competitor species.

Figure 11.9 A “Natural Experiment” on Competition between Chipmunks



Competitive Exclusion

Concept 11.3: Competing species are more likely to coexist when they use resources in different ways.

If the overall ecological requirements of a species—its *ecological niche*—are very similar to those of a superior competitor, that competitor may drive it to extinction.

Competitive Exclusion

In the 1930s, G. F. Gause performed laboratory experiments on competition using three species of *Paramecium*.

Populations of all three *Paramecium* species reached a stable carrying capacity when grown alone.

When paired, some species drove others to extinction.

Figure 11.10 Competition in *Paramecium* (Part 1)

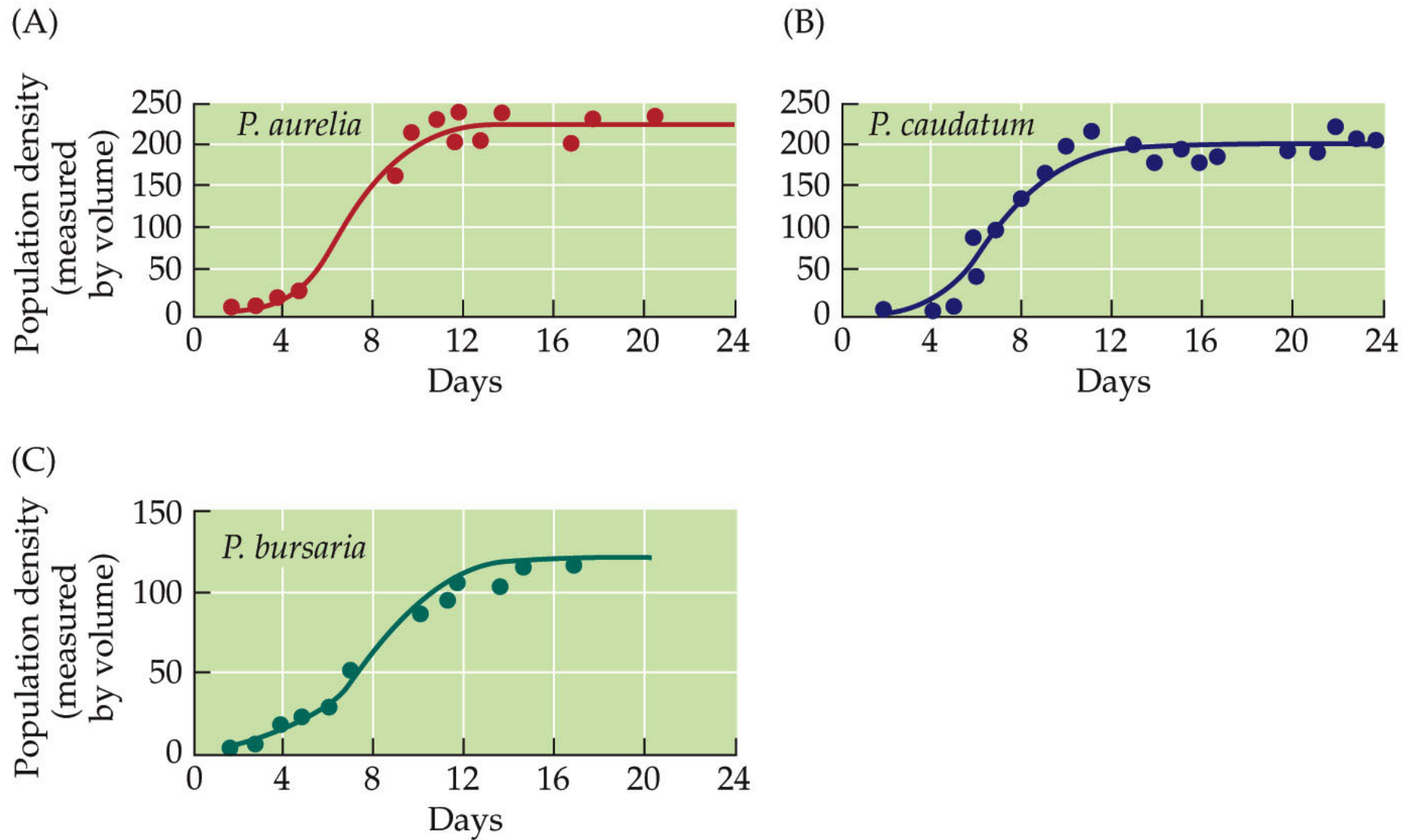
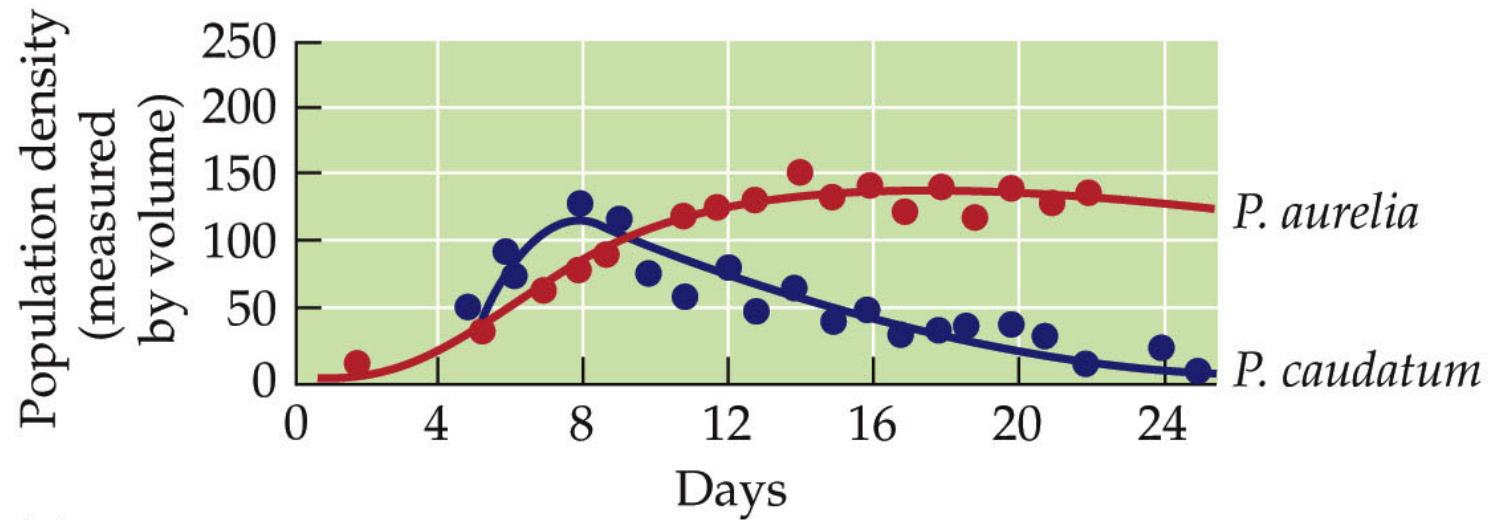
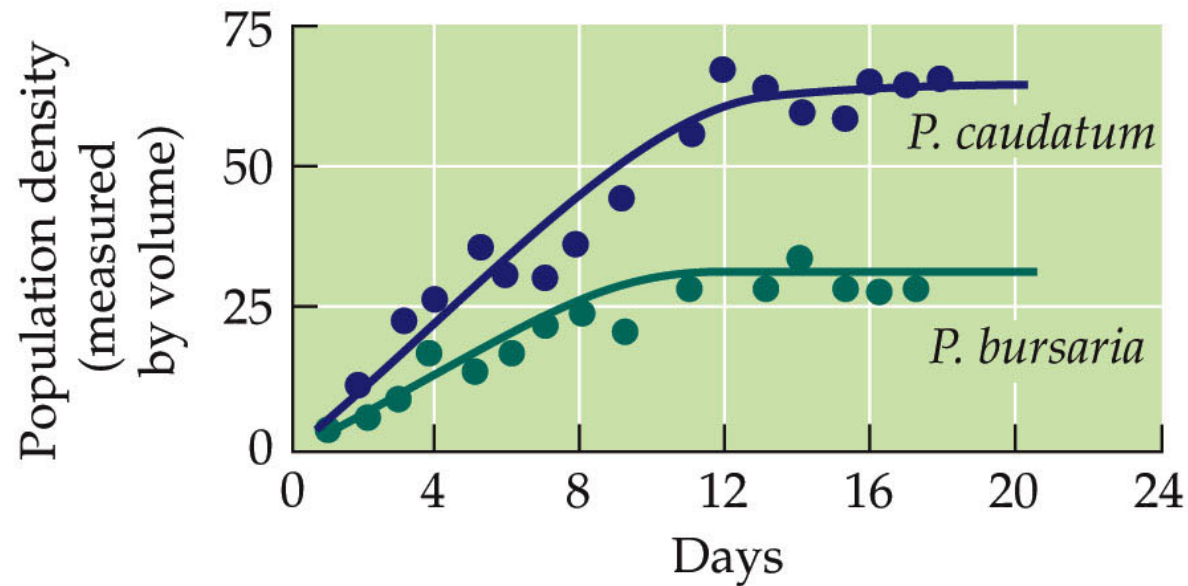


Figure 11.10 Competition in *Paramecium* (Part 2)

(D)



(E)



Competitive Exclusion

P. aurelia drove *P. caudatum* to extinction. They may have been unable to coexist because both fed on bacteria floating in the medium.

P. caudatum and *P. bursaria* were able to coexist, although they were clearly in competition—the carrying capacity of both species was lowered.

Competitive Exclusion

P. caudatum usually ate bacteria floating in the medium, while *P. bursaria* usually fed on yeast cells that settled to the bottom.

Unless two species use available resources in different ways, one can go extinct.

Competitive Exclusion

The **competitive exclusion principle**:

Two species that use a limiting resource in the same way can not coexist.

Field observations are consistent with this explanation of why competitive exclusion occurs in some cases, but not others.

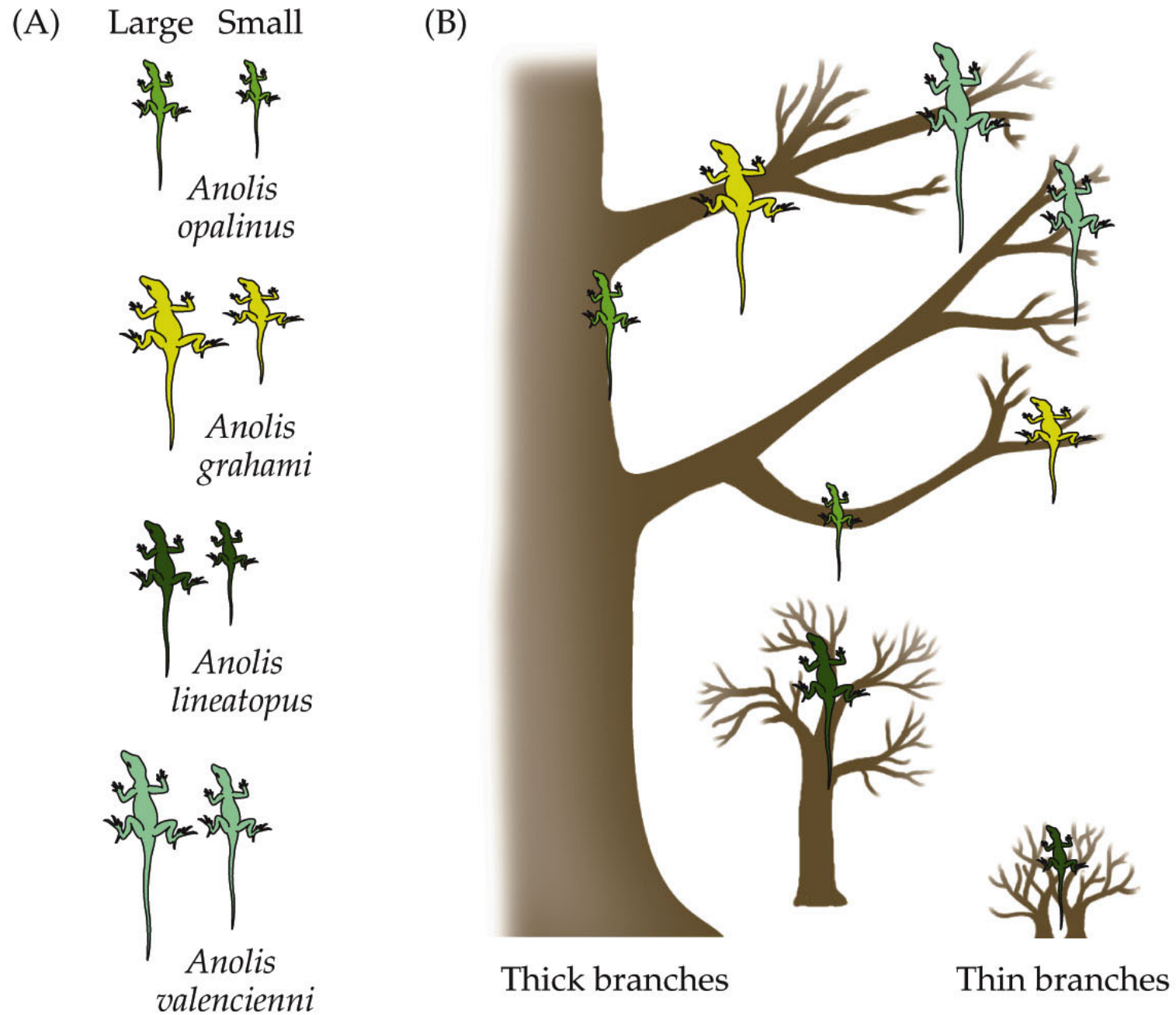
Competitive Exclusion

Resource partitioning: Species use a limited resource in different ways.

Example: Four species of *Anolis* lizards on Jamaica live together in trees and shrubs and eat similar food.

Schoener (1974) found that the lizards used the space in different ways, resulting in a reduction in competition.

Figure 11.11 Resource Partitioning in Lizards



Competitive Exclusion

Competition was first modeled by A. J. Lotka (1932) and Vito Volterra (1926).

Their equation is now known as the **Lotka–Volterra competition model**.

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{(N_1 + \alpha N_2)}{K_1} \right)$$
$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{(N_2 + \beta N_1)}{K_2} \right)$$

Competitive Exclusion

N_1 = population density of species 1

r_1 = intrinsic rate of increase of species 1

K_1 = carrying capacity of species 1

α and β = **competition coefficients**—
constants that describe effect of one
species on the other:

Box 11.1 What Do the Competition Coefficients α and β Represent?

α is the effect of species 2 on species 1;
 β is the effect of species 1 on species 2.

α measures the extent to which the use of resources by an individual of species 2 decreases the per capita growth rate of species 1.

When $\alpha = 1$, individuals of the two species are identical in their effects.

Box 11.1 What Do the Competition Coefficients α and β Represent?

When $\alpha < 1$, an individual of species 2 decreases growth of species 1 by a *smaller* amount than does an individual of species 1.

When $\alpha > 1$, an individual of species 2 decreases growth of species 1 by a *larger* amount than does an individual of species 1.

Competitive Exclusion

The Lotka–Volterra model supports the idea that competitive exclusion is likely when competing species require very similar resources.

The model can be used to predict changes in the densities of species 1 and 2 over time. Then those changes can be related to the way in which each species uses resources.

Box 11.2 When Do Competing Populations Stop Changing in Size?

Population density of species 1 does not change over time when $dN_1/dt = 0$.

This can occur when

$$\left(1 - \frac{(N_1 + \alpha N_2)}{K_1}\right) = 0$$

rearranging:

$$N_2 = \frac{K_1}{\alpha} - \frac{1}{\alpha} N_1$$

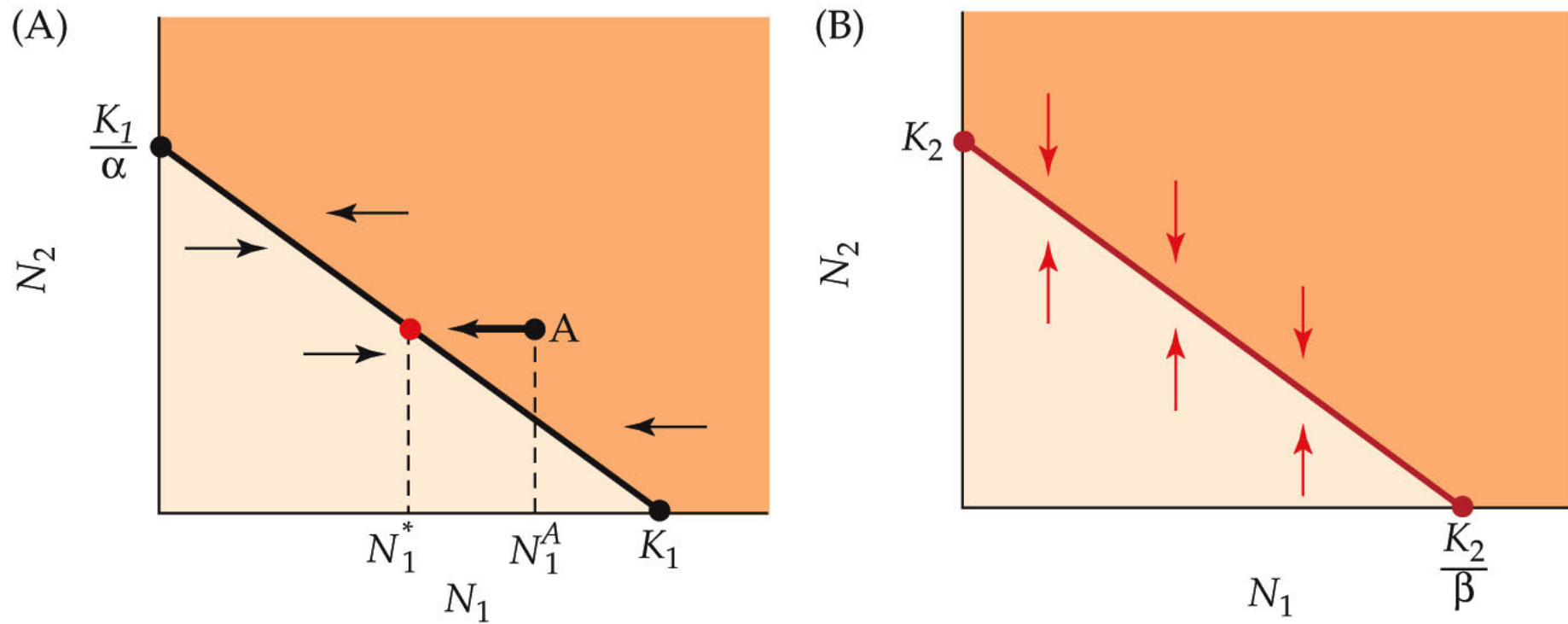
Box 11.2 When Do Competing Populations Stop Changing in Size?

Using a similar approach for species 2, we find that $dN_2/dt = 0$ when

$$N_2 = K_2 - \beta N_1$$

These two equations describe straight lines written with N_2 as a function of N_1 .

Figure 11.12 Graphical Analyses of Competition



Competitive Exclusion

The straight lines are **zero population growth isoclines**: The population does not increase or decrease in size for any combination of N_1 and N_2 that lies on these lines.

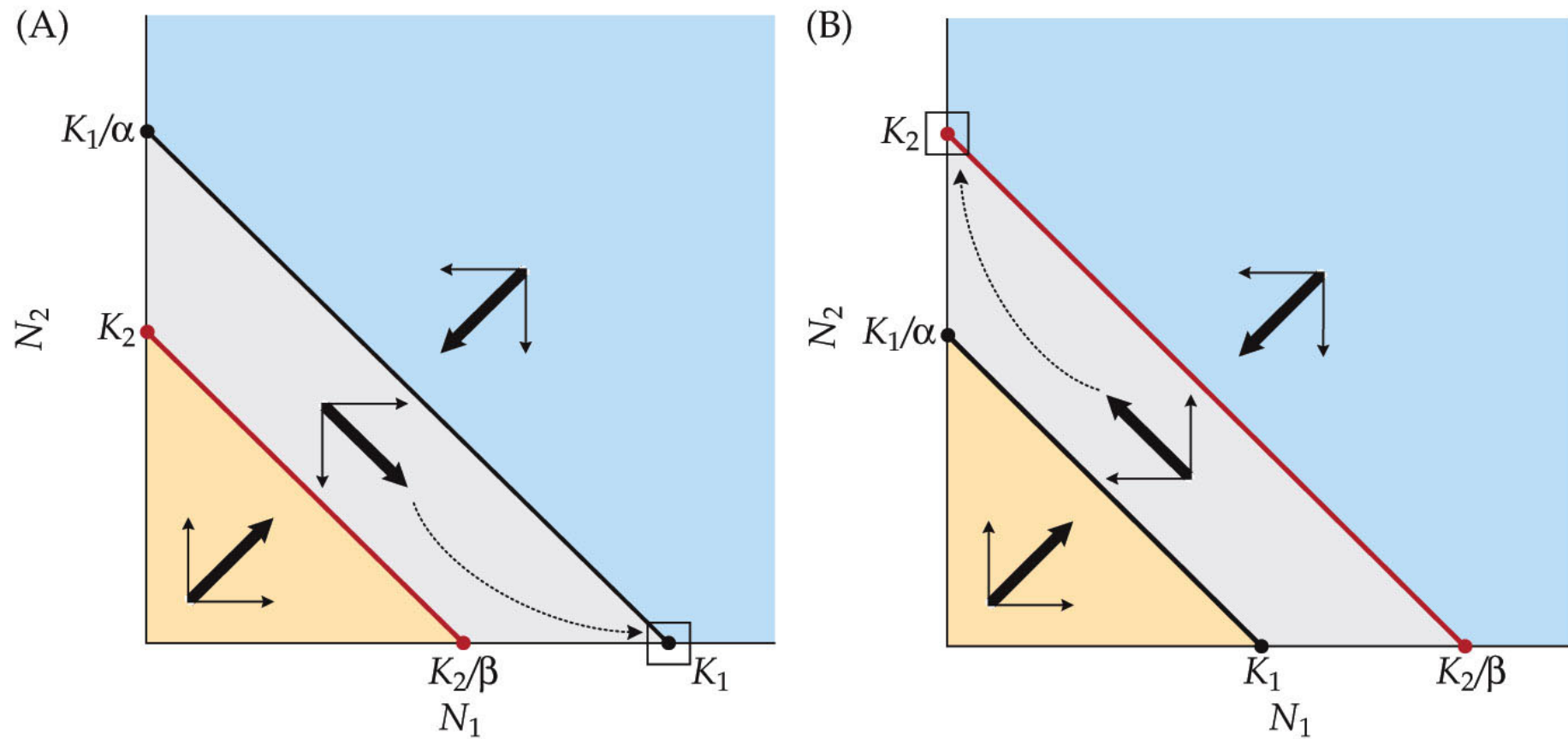
Zero growth isoclines can determine the conditions under which each species will increase or decrease.

Competitive Exclusion

This graphical approach can be used to predict the end result of competition between species.

The N_1 and N_2 isoclines are plotted together. There are four possible ways that the N_1 and N_2 isoclines can be arranged relative to each other.

Figure 11.13 A, B Outcome of Competition in the Lotka–Volterra Competition Model

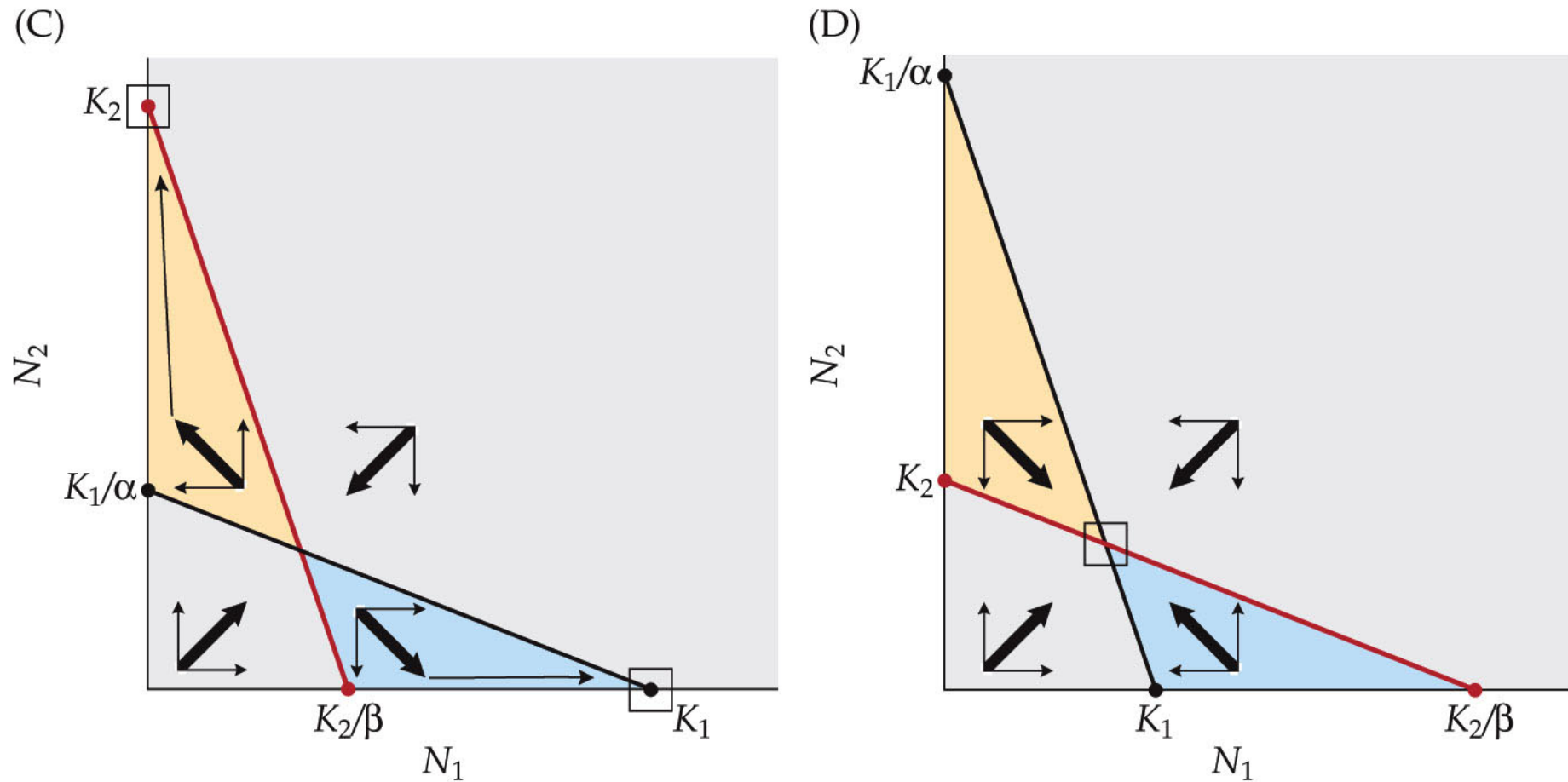


Competitive Exclusion

When the isoclines do not cross,
competitive exclusion results.

Depending on which isocline is above the
other, either species 1 or species 2
always drives the other to extinction.

Figure 11.13 C, D Outcome of Competition in the Lotka–Volterra Competition Model



Competitive Exclusion

In only one case, the two species coexist.

Although in this case, competition still has an effect: The final or equilibrium density of each species is lower than its carrying capacity.

Competitive Exclusion

Coexistence occurs when the values of α , β , K_1 , and K_2 are such that the following inequality holds:

$$\alpha < \frac{K_1}{K_2} < \frac{1}{\beta}$$

If α and β are equal, and close to 1, the species are equally strong competitors, and have similar effects on each other.

Competitive Exclusion

Example: If $\alpha = \beta = 0.95$

$$0.95 < \frac{K_1}{K_2} < 1.053$$

Coexistence is predicted only within a narrow range of values for the carrying capacities, K_1 and K_2 .

Competitive Exclusion

Example: If $\alpha = \beta = 0.1$

$$0.1 < \frac{K_1}{K_2} < 10$$

Coexistence is predicted within a much broader range of carrying capacities.

Altering the Outcome of Competition

Concept 11.4: The outcome of competition can be altered by environmental conditions, species interactions, disturbance, and evolution.

Environmental conditions can results in a *competitive reversal*—the species that was the inferior competitor in one habitat becomes the superior competitor in another.

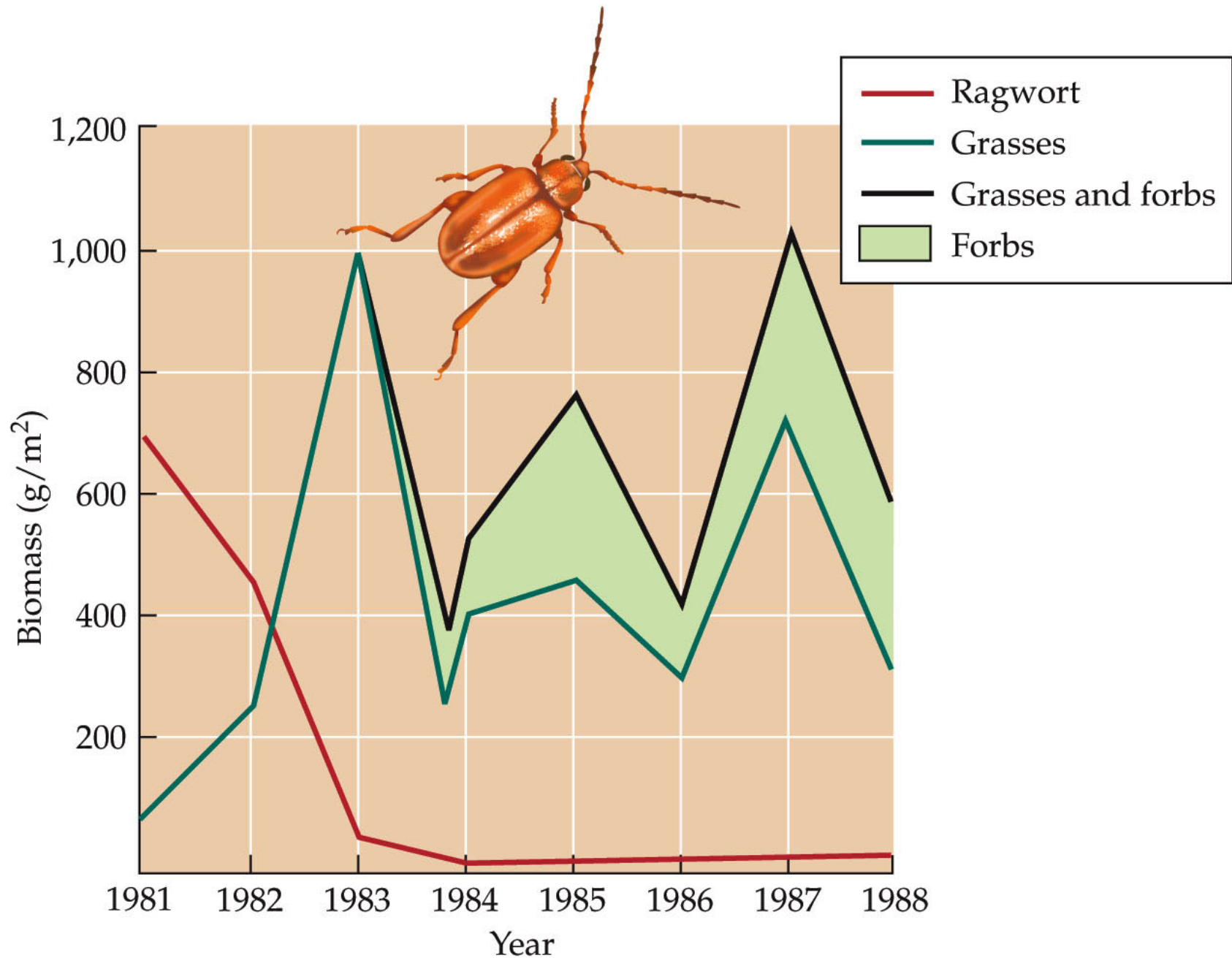
Altering the Outcome of Competition

Example: Presence of herbivores can lead to competitive reversals.

When ragwort flea beetles were introduced to western Oregon, the biomass of ragwort, an invasive species, decreased, and its competitor species increased.

In the absence of the flea beetles, ragwort is a superior competitor.

Figure 11.14 Herbivores Can Alter the Outcome of Competition



Altering the Outcome of Competition

Disturbances such as fires or storms can kill or damage individuals, while creating opportunities for others.

Example: Some forest plant species require abundant sunlight and are found only where disturbance has opened the tree canopy.

As trees recolonize and create shade, these plants can not persist in the patch.

Altering the Outcome of Competition

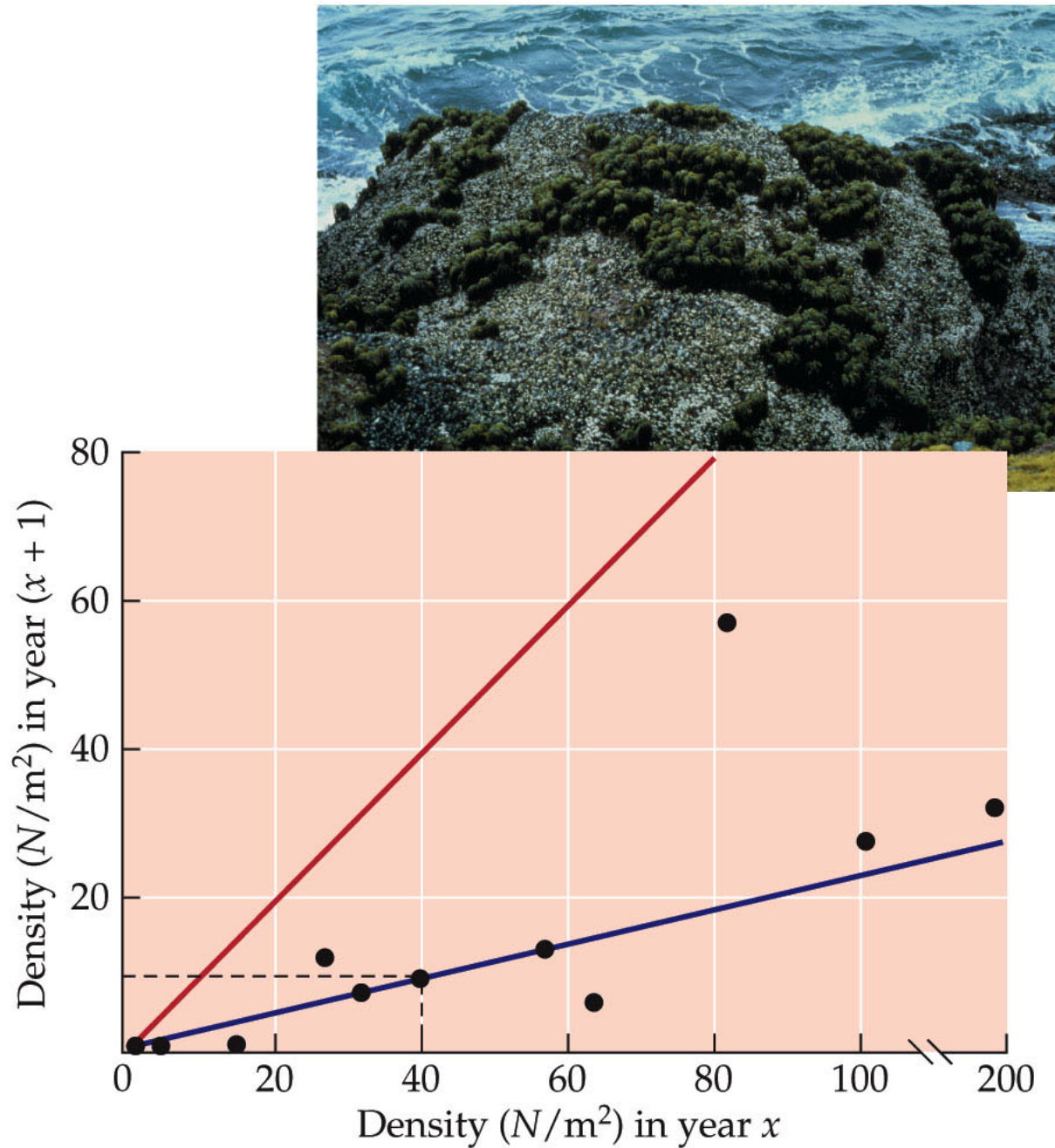
Such species are called **fugitive species** because they must disperse from one place to another as conditions change.

The brown alga called sea palm coexists with mussels, a competitively dominant species, in the rocky intertidal zone because large waves sometimes remove the mussels, creating temporary openings.

Altering the Outcome of Competition

On shorelines with low disturbance rates, competition runs its course, and mussels drive sea palms to extinction.

Figure 11.15 Population Decline in an Inferior Competitor



Altering the Outcome of Competition

Competition has the potential to cause evolutionary change, and evolution has the potential to alter the outcome of competition.

This interplay has been observed in many studies.

Altering the Outcome of Competition

In experimental studies of competing fly species, house flies and green blowflies were grown together in chambers and given the same food.

Initially, houseflies appeared to be the superior competitors, rapidly increasing in density.

Over time, the situation reversed, and eventually the houseflies went extinct.

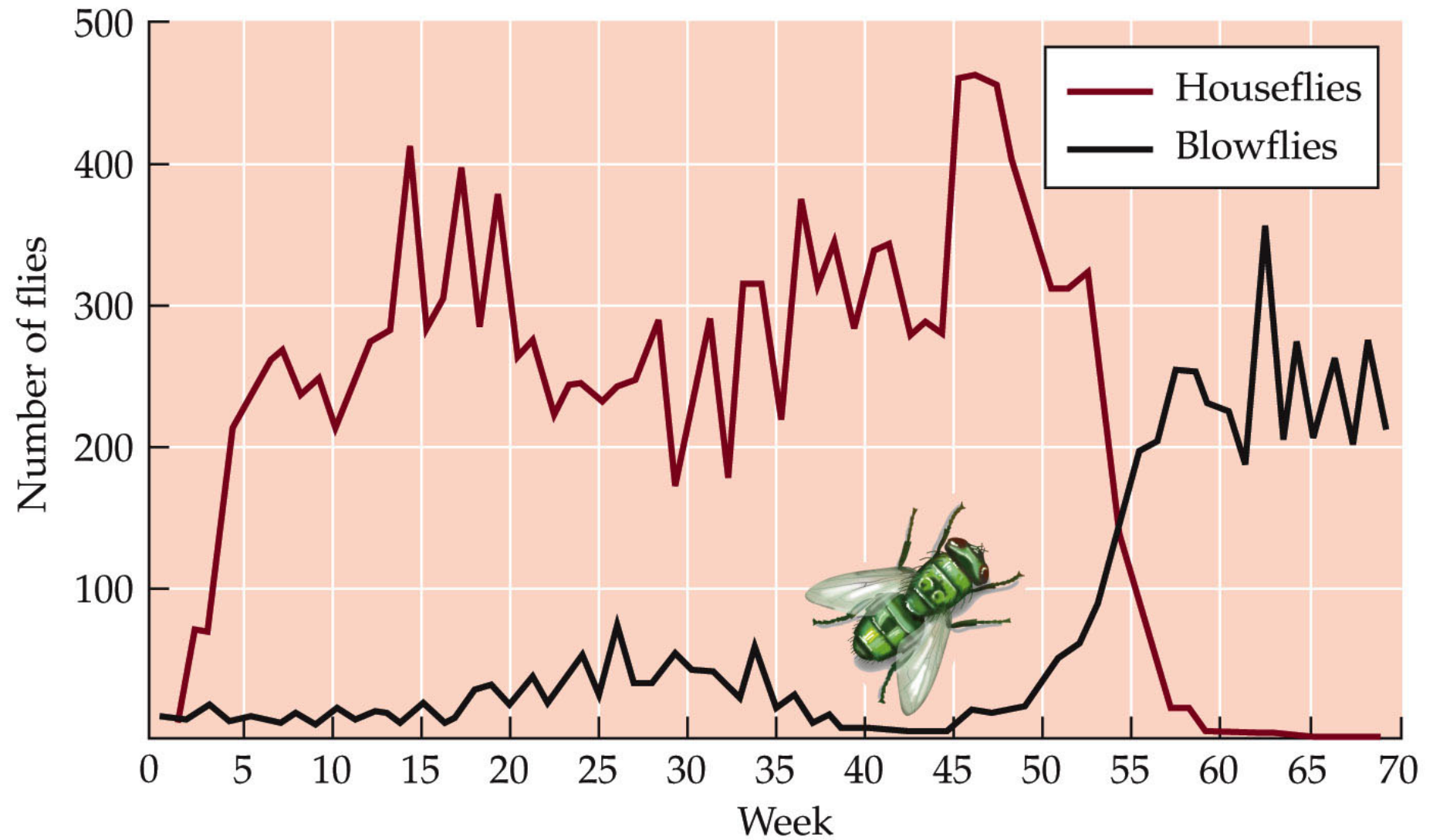
Figure 11.16 A Competitive Reversal (Part 1)

(A)



Figure 11.16 A Competitive Reversal (Part 2)

(B)



Altering the Outcome of Competition

Individuals were also tested for signs of evolutionary change.

Blowflies raised in competition with houseflies had evolved to become superior competitors and always outcompeted the houseflies.

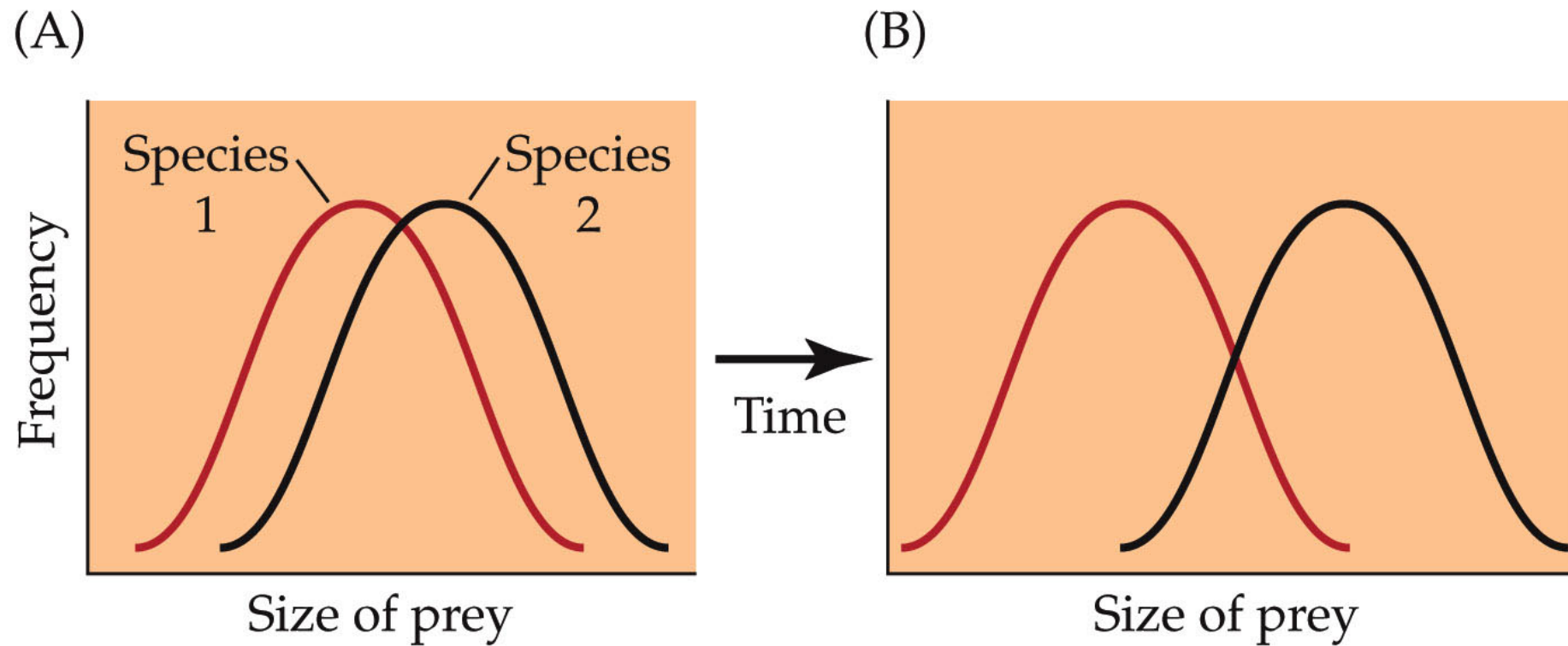
The underlying mechanisms of this and the associated genetic changes are not known.

Altering the Outcome of Competition

Natural selection can influence the morphology of competing species and result in **character displacement**.

Natural selection results in the forms of competing species becoming more different over time.

Figure 11.17 Character Displacement



Altering the Outcome of Competition

In two species of finches on the Galápagos archipelago, the beak sizes, and hence sizes of the seeds the birds eat, are different on islands with both species.

On islands with only one of the species, beak sizes are similar.

Figure 11.18 Competition Shapes Beak Size (Part 1)

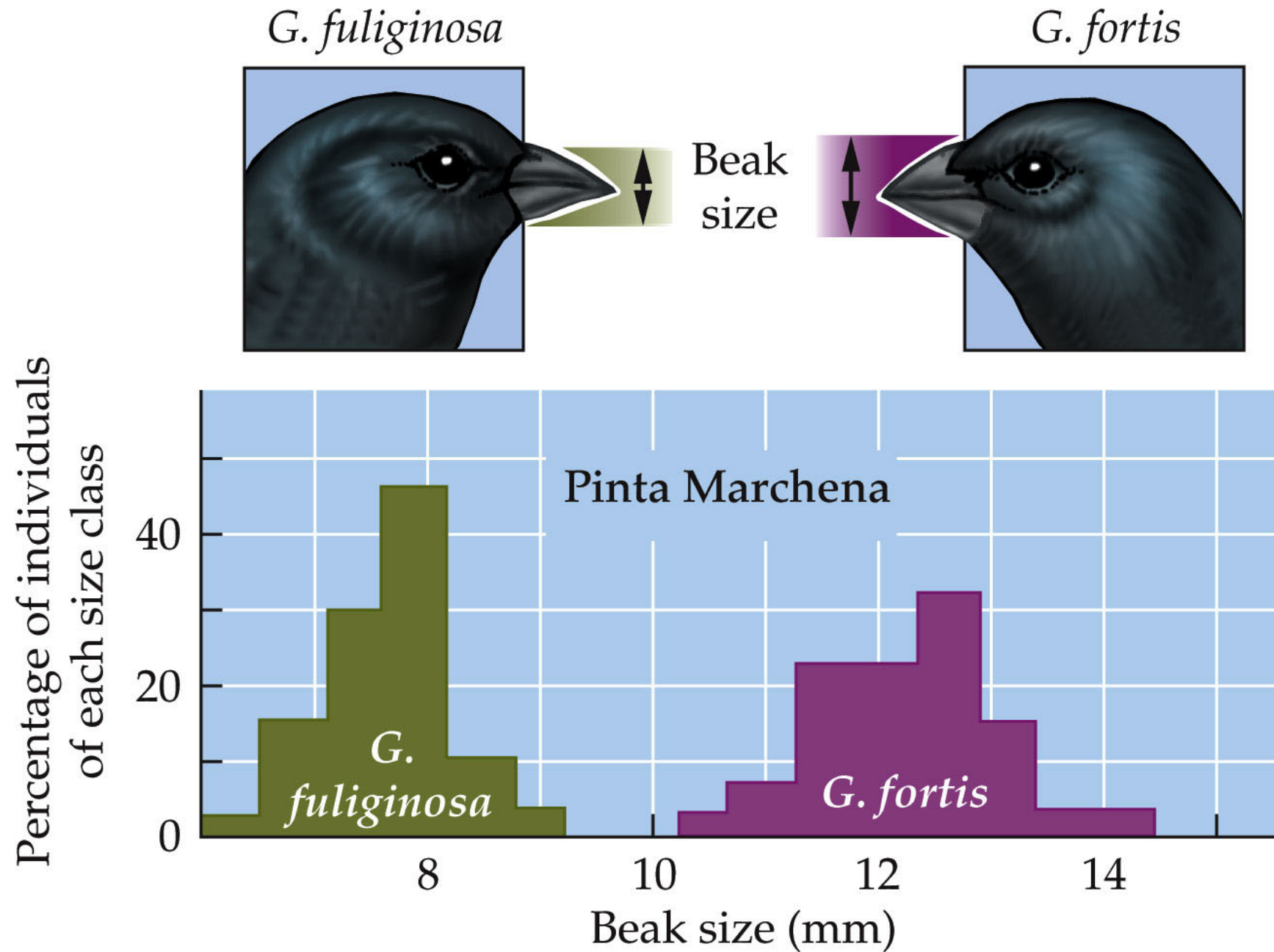
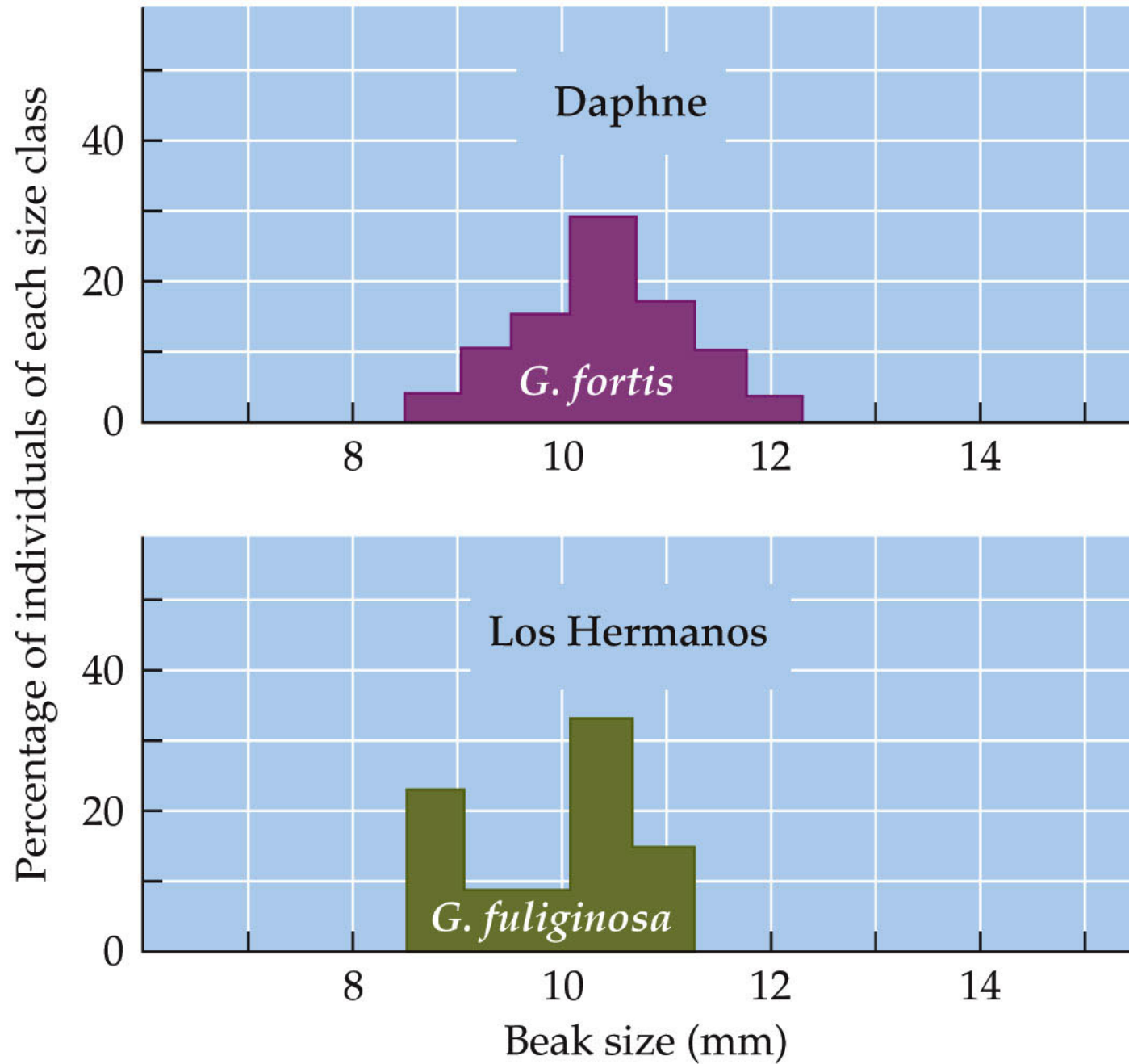


Figure 11.18 Competition Shapes Beak Size (Part 2)



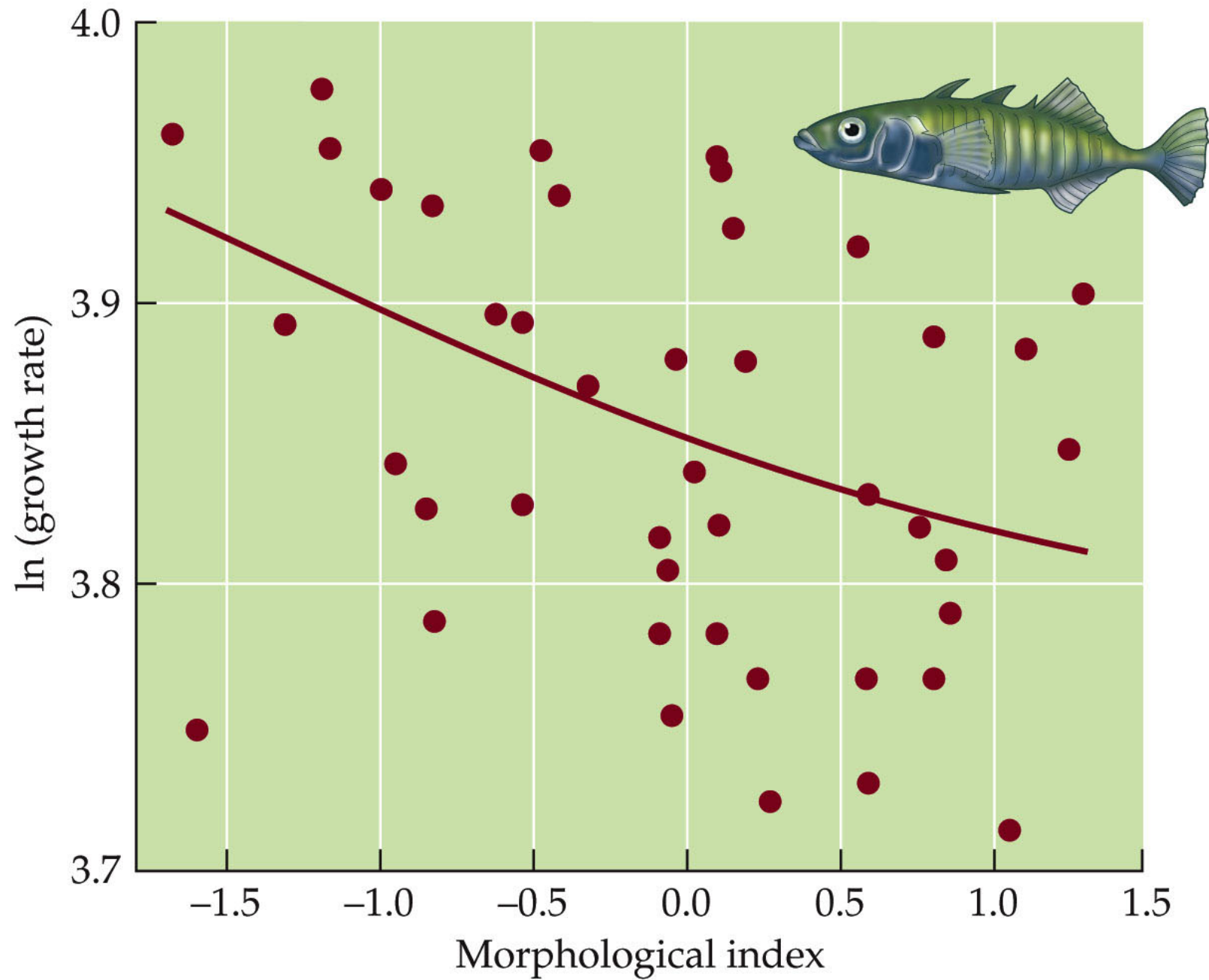
Altering the Outcome of Competition

Experimental studies have also demonstrated character displacement.

The morphology of sticklebacks (fish) varies the most when different species live in the same lake.

Individuals whose morphology differed considerably from their competitors grew more rapidly than did those with morphology similar to that of their competitors.

Figure 11.19 An Experimental Test of Character Displacement



Case Study Revisited: Competition in Plants that Eat Animals

In the experimental studies on pitcher plants (*S. alata*), the results suggested little competition between the pitcher plant and its noncarnivorous neighbors for soil nutrients.

But competition for light was more important. When shaded by neighbors, pitcher height increased at the expense of pitcher volume.

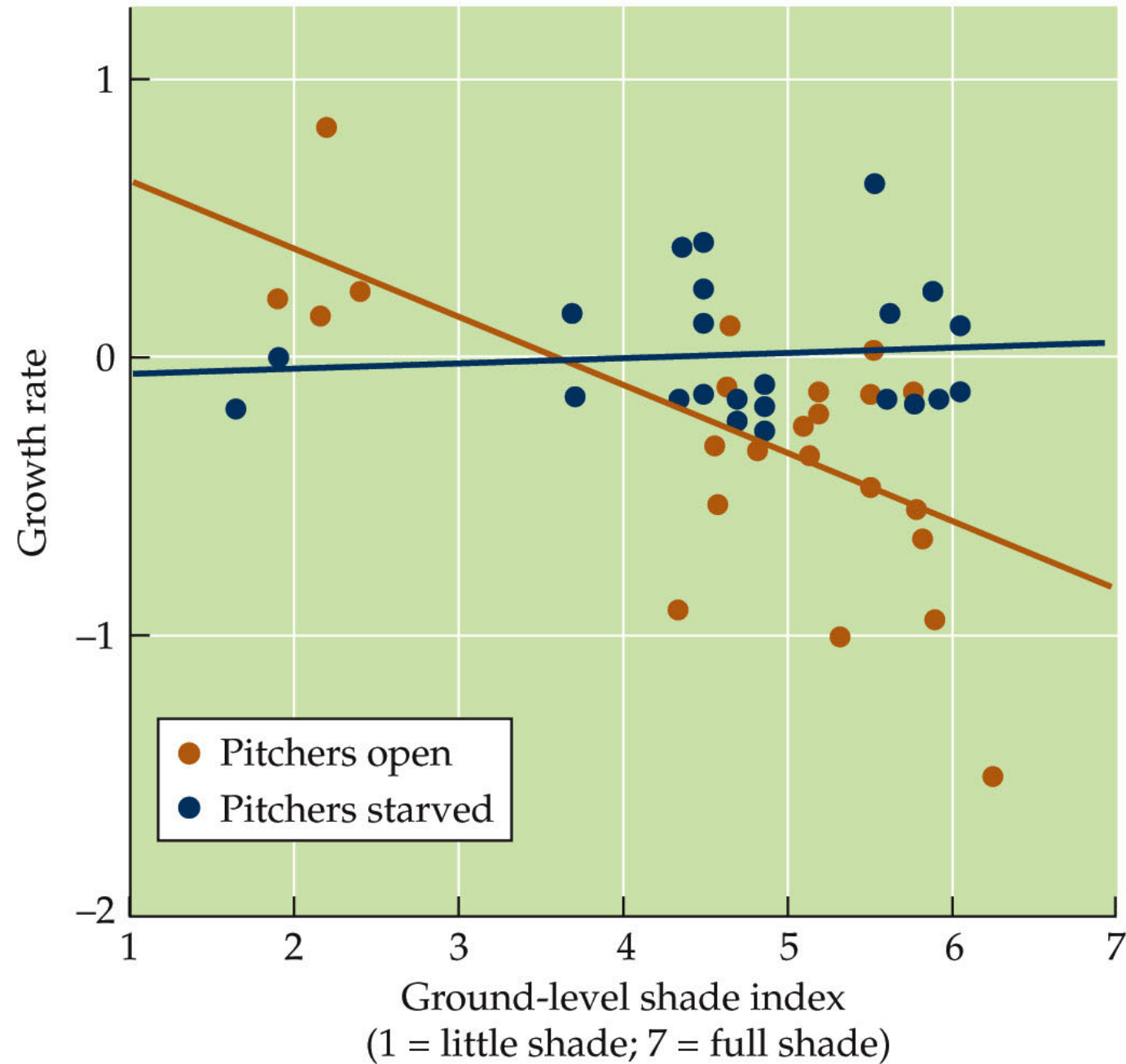
Case Study Revisited: Competition in Plants that Eat Animals

When neighbors were removed, *S. alata* growth rate increased, but only when they were able to capture animal prey.

When neighbors were left intact, light availability had no effect on *S. alata* growth rates when prey were excluded.

When prey was available, growth rate increased as light increased.

Figure 11.20 Interaction between Light and Prey Availability



Case Study Revisited: Competition in Plants that Eat Animals

S. alata competes with its neighbors for light but avoids competition for soil nutrients by eating animal prey.

When light levels are low, *S. alata* grows little and requires few nutrients, thus prey deprivation has little effect.

In high light levels, *S. alata* grows more and requires nutrients, thus prey deprivation matters.

Connections in Nature: The Paradox of Diversity

In spite of competition, natural communities contain many species sharing scarce resources.

Resource partitioning is one explanation for this.

Other mechanisms include environmental variation and disturbance. Species may coexist if different species are superior competitors under different environmental conditions.

Connections in Nature: The Paradox of Diversity

In the pitcher plant studies, Brewer wanted to know whether resource partitioning in the form of different methods of nutrient acquisition could explain the coexistence of carnivorous and noncarnivorous plants.

Connections in Nature: The Paradox of Diversity

When pitcher plants were deprived of prey, they should have experienced more severe competitive effects, or compensated for reduced nutrients by increasing production of roots or pitchers.

Neither of these outcomes occurred.

Connections in Nature: The Paradox of Diversity

S. alata is tolerant of fire and uses changes in light levels as a cue for growth.

It grows primarily when its competitors are absent or reduced (e.g., after a fire).

This growth strategy may allow *S. alata* to persist with noncarnivorous plants that can outcompete it for both light and scarce soil nutrients.