18

Species Diversity in Communities

18 Species Diversity in Communities

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The first automobile was built in 1889, just as the last covered wagons crossed the American prairies.

Millions of cars now dominate our lives, but they have many negative environmental impacts, such as CO_2 emissions.

Figure 18.1 Powered by Prairies?

Case Study: Powered by Prairies? Biodiversity and Biofuels

Dwindling supplies of fossil fuels has led to development of **biofuels**—liquid or gas fuels from plant material (biomass).

In the U.S., ethanol is made from corn, while biodiesel is made from soybeans.

Ideally, biofuels are **carbon neutral**—the amount of CO_2 produced by burning them is matched by the amount taken up by the plants from which they are made.

They are a nearly limitless renewable resource, as long as the crops can be grown.

Biofuels have many downsides as well.

Growing corn and soybeans for biofuels competes for land and water that could be used for growing food.

Fossil fuels, in the form of fertilizers and pesticides, and for farm work, are required to grow these crops.

A promising possibility is to use non-edible plants (or plant parts), such as corn stalks, straw, or waste wood, to make biofuels.

Most of the land that was once prairie in North America has been converted to agriculture. Much of this is now degraded and not suitable for high-yield food crops.

Case Study: Powered by Prairies? Biodiversity and Biofuels

Studies at Cedar Creek, Minnesota suggest that a diverse assemblage of prairie plants could be grown on such land, and become a source of biomass for biofuel production.

David Tillman has studied prairie plant species diversity in abandoned agricultural land.

Figure 18.2 Plant Diversity Matters

ECOLOGY, Figure 18.2

Experiments showed that plots with more plant species produced greater biomass for a given amount of water or nutrients than plots with fewer species.

Growing prairie plants would require lower inputs of fossil fuels than traditional crop plants.

Introduction

This chapter focuses on species diversity at the local scale, and also on two important questions:

- What are the factors that control species diversity within communities?
- What is the function of this species diversity within communities?

Concept 18.1: Species richness differs among communities due to variation in regional species pools, abiotic conditions, and species interactions.

If you looked across a landscape from the top of a mountain you would see a patchwork of different communities, each with a different species composition and species richness.

Figure 18.3 A View from Above

Distribution and abundance of species in communities is dependent on:

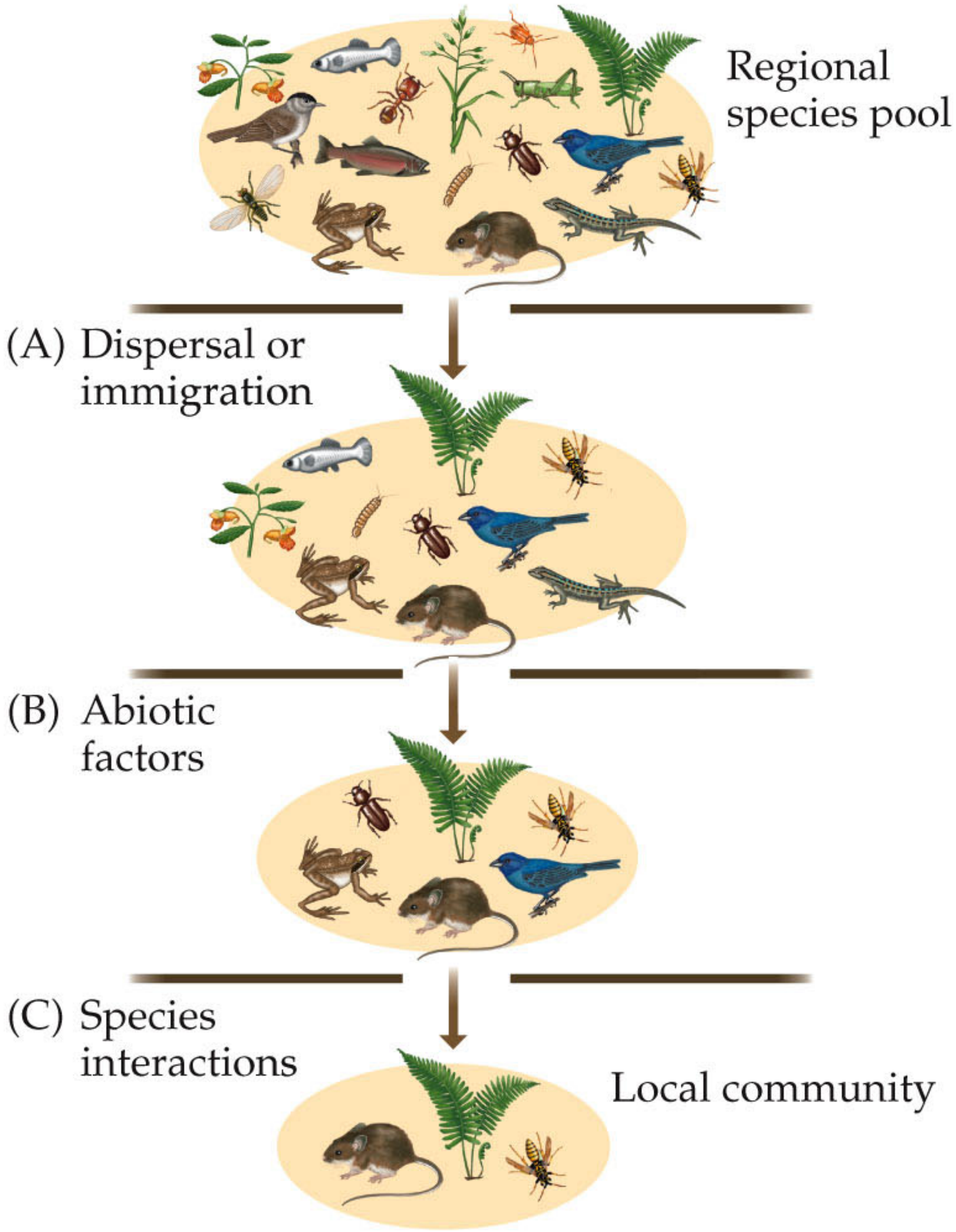
1. Regional species pools and dispersal ability.

2. Abiotic conditions.

3. Species interactions.

These factors act as “filters,” which exclude species from (or include species in) particular communities.

Figure 18.4 Community Membership: A Series of Filters



Community Membership

1. The regional species pool provides an upper limit on the number and types of species that can be present in a community.

The importance of dispersal can be seen in cases of non-native species invasions.

Community Membership

Humans have greatly expanded the regional species pools of communities by serving as vectors of dispersal.

Example: Aquatic species travel to distant parts of the world in ballast water carried by ships.

Water, along with aquatic organisms, is pumped into and out of ships' ballast tanks all over the world.

Figure 18.5 A Humans Are Vectors for Invasive Species

(A)

Ballast water introductions have increased over the past few decades because ships are larger and faster; more species can be taken along and survive the trip.

The zebra mussel (*Dreissena polymorpha*), arrived in the Great Lakes in ballast water in the late 1980s.

Figure 18.5 B, C Humans Are Vectors for Invasive Species

(B)

Community Membership

Zebra mussels spread quickly, and have had community-changing effects by fouling infrastructure and dramatically changing water properties.

Densities as high as 700,000 / m^2 have been recorded; their filter feeding has decreased phytoplankton populations by 80%–90%.

Community Membership

The comb jelly *Mnemiopsis leidyi* was introduced into the Black Sea via ballast water, with many negative consequences.

These and other damaging invasions have made it clear that ecologists cannot ignore the role of large-scale processes of dispersal in determining species richness at the local scale.

2. A species may be able to reach a community but be physiologically unable to tolerate the abiotic conditions of the environment.

Some abiotic constraints are obvious (e.g., an aquatic habitat would not support terrestrial plants, or a lake might not support organisms that require fast-flowing water).

Community Membership

There are many examples of physiological constraints on the distribution and abundance of species.

Many species that are dispersed in ballast water are unable to survive in a new habitat because of temperature, salinity, or other factors.

But, as in the case of *Caulerpa* in the Mediterranean Sea, we cannot rely on physiological constraints as a mechanism to exclude potential invaders.

With multiple introductions, some individuals with slightly different physiology could survive and reproduce in an environment once thought uninhabitable by their species.

Community Membership

3. The final cut requires coexistence with other species.

For species that depend on other species for growth, reproduction, or survival, those other species must be present.

Species may be excluded from a community by competition, predation, parasitism, or disease.

Some non-native species do not become part of the new community.

This may be due to **biotic resistance**—when interactions with the native species exclude the invader.

Example: Native herbivores can reduce the spread of non-native plants, but can they completely exclude them?

Community Membership

In Australia, adults and larvae of a native moth breed and feed on seed pods of the invasive gorse shrub, but the plant continues to spread.

Not a lot is known about biotic resistance, partly because failed introductions of non-native species tend to go completely undetected.

Figure 18.6 Stopping Gorse Invasion?

Community Membership

There are two schools of thought on how species coexist in a community:

- **Equilibrium theory**—ecological and evolutionary compromises lead to resource partitioning.

- **Nonequilibrium theory**—fluctuating conditions keep dominant species from monopolizing resources.

Resource Partitioning

Concept 18.2: Resource partitioning among the species in a community reduces competition and increases species richness.

Resource partitioning—competing species are more likely to coexist when they use resources in different ways.

In a simple model of resource partitioning, each species' resource use falls on a spectrum of available resources.

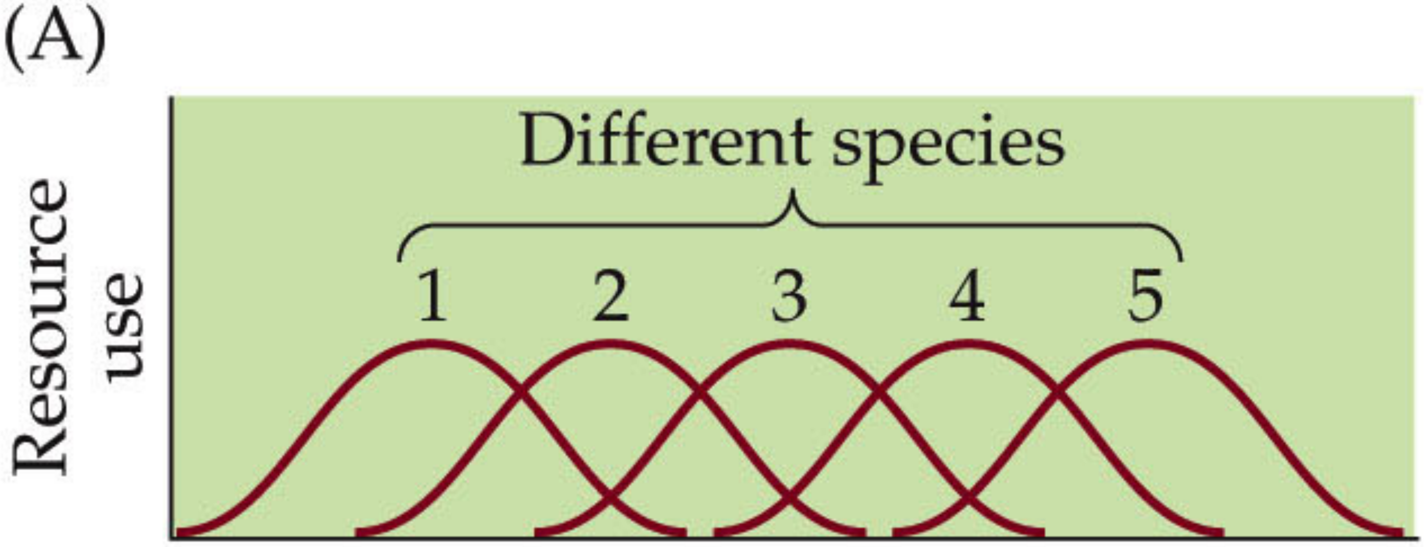


Figure 18.7 A Resource Partitioning

Resource Partitioning

A species' resource use may overlap with that of other species.

The more overlap, the more competition between species.

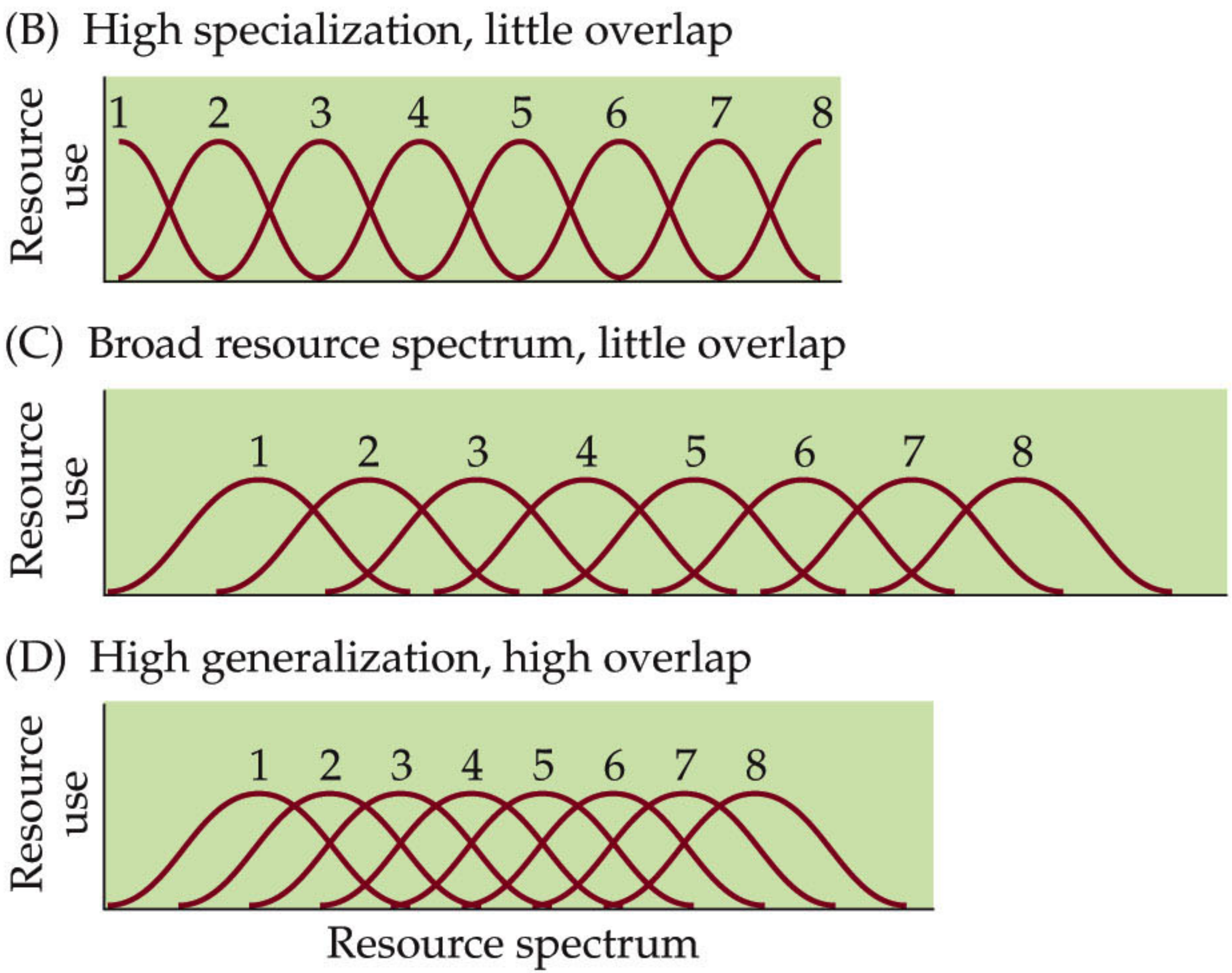
The less overlap, the more specialized species have become, and the less strongly they compete.

Resource Partitioning

Species that show a high degree of specialization along the resource spectrum can result in high species richness in some communities.

More species can be “packed” into a community with little overlap.

Figure 18.7 B, C, D Resource Partitioning



Resource Partitioning

Species richness can also be high if the resource spectrum is broad.

Or, species richness could be high if species were generalists with high overlap of resource use. There would be more competition, and smaller population sizes, but more species could be packed into the community.

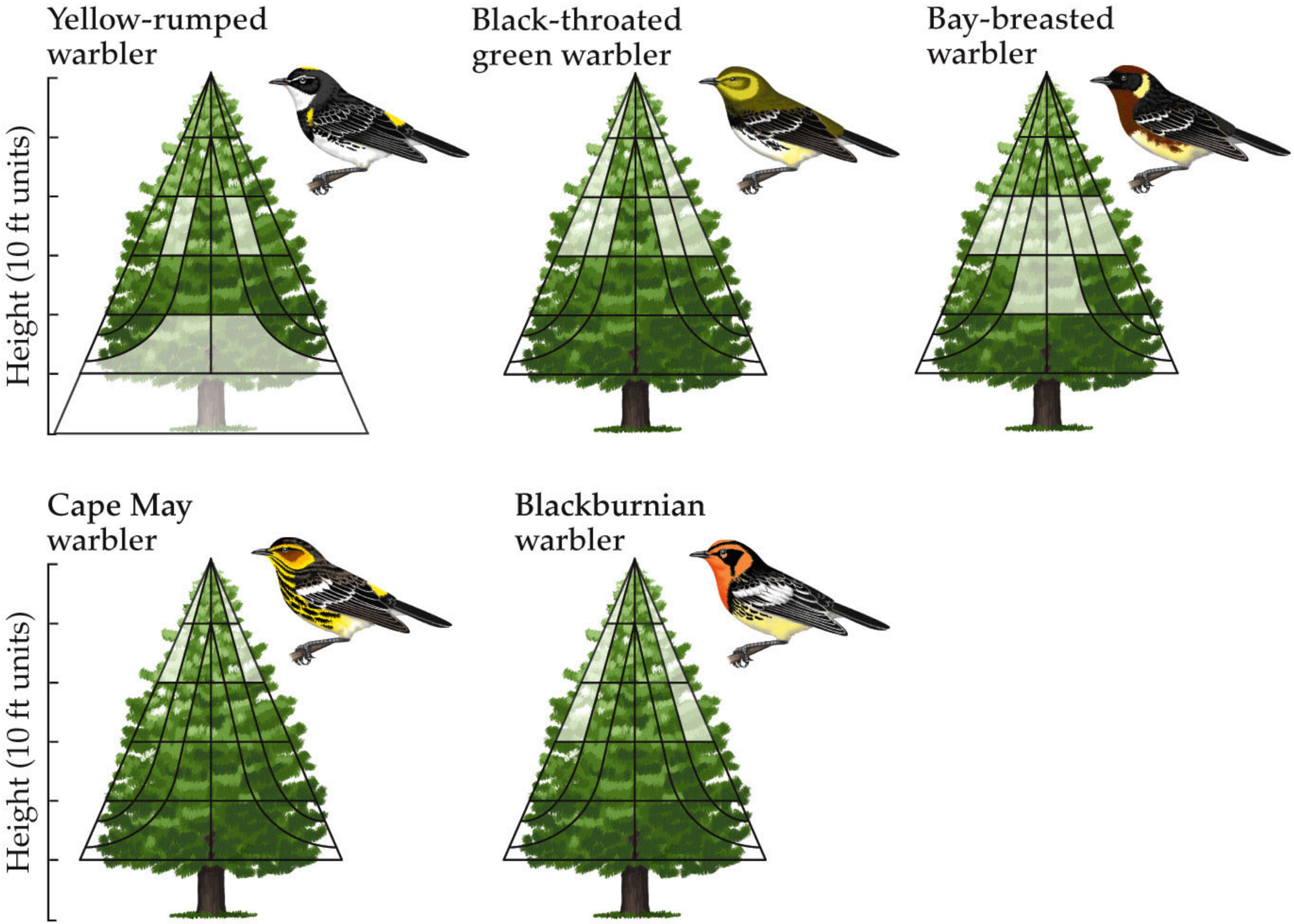
Resource Partitioning

MacArthur (1958) looked at resource partitioning in whole communities.

He studied five species of warblers in New England forests, recording feeding habits, nesting locations, and breeding territories.

When he mapped the locations of warbler activity he found that the birds were using different parts of the habitat in different ways.

Figure 18.8 Resource Partitioning by Warblers



ECOLOGY, Figure 18.8

Resource Partitioning

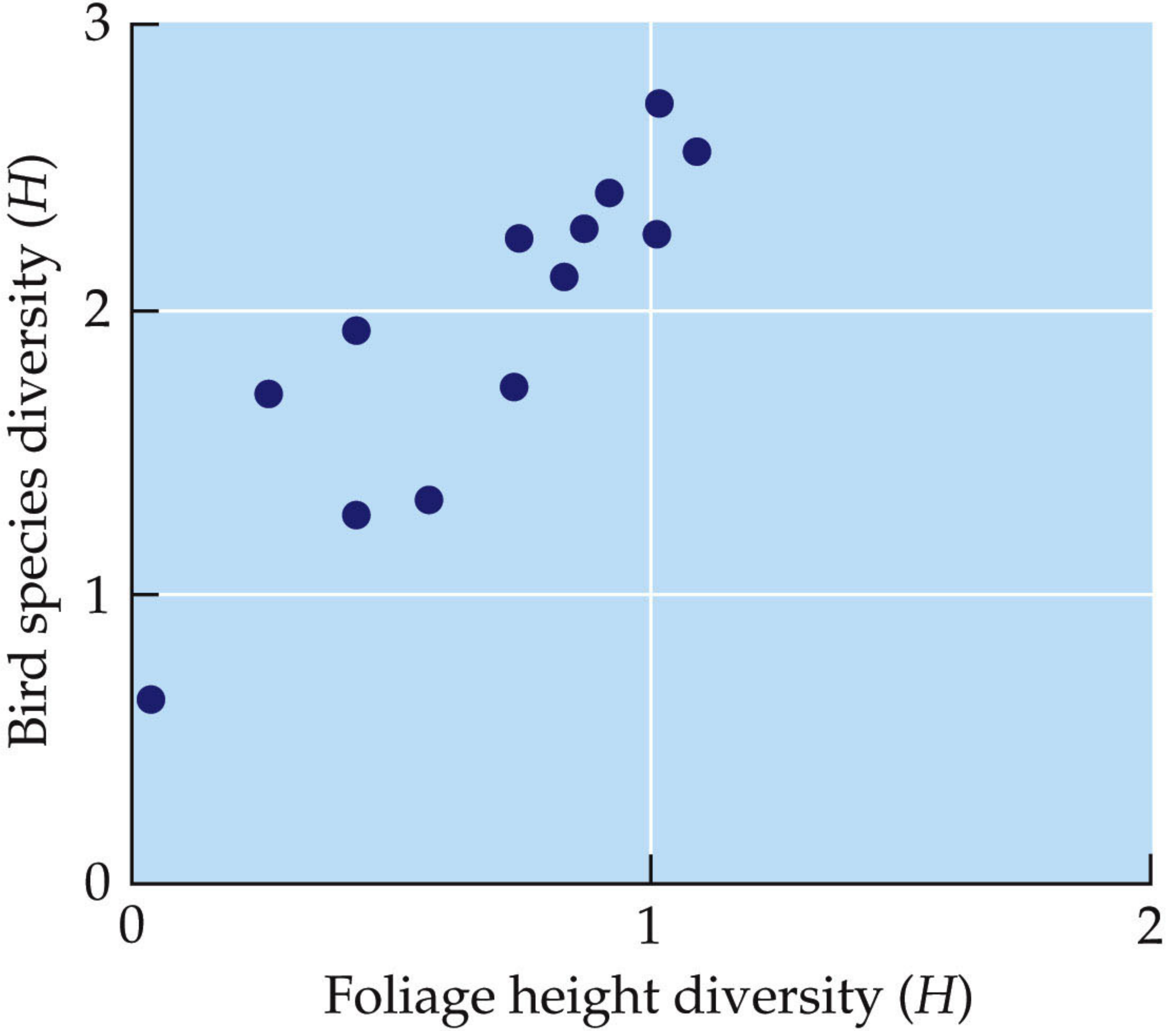
MacArthur found that the nesting heights and breeding territories of the five warbler species also varied.

Resource Partitioning

In further studies, MacArthur and MacArthur (1961) looked at bird communities in 13 different habitats.

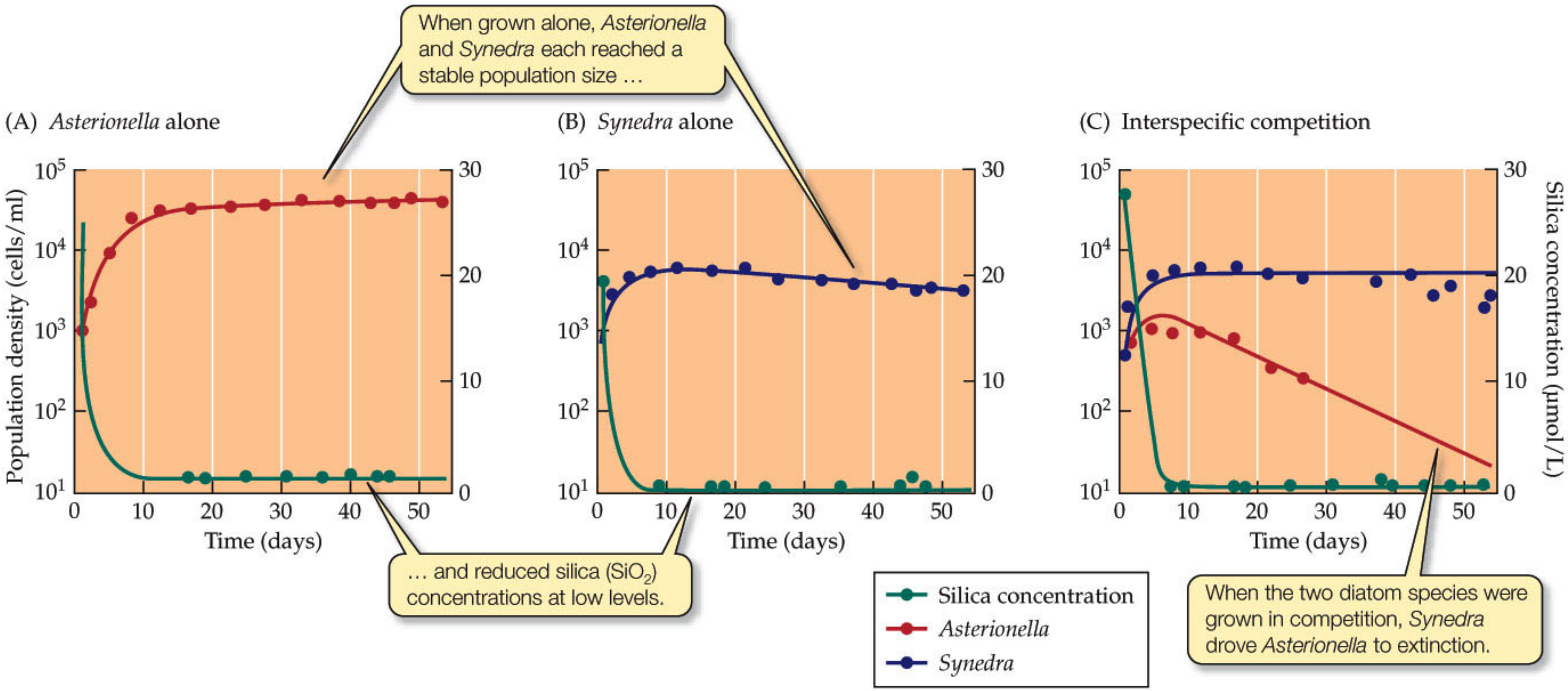
There was a positive relationship between bird species diversity and foliage height diversity (number of vegetation layers, an indication of habitat complexity).

Figure 18.9 Bird Species Diversity Is Higher in More Complex Habitats



ECOLOGY, Figure 18.9

Recall Tillman's experiments with two species of diatoms that competed for silica.



Resource Partitioning

To explain how diatom species coexist in nature, he proposed the **resource ratio hypothesis**—species coexist by using resources in different proportions.

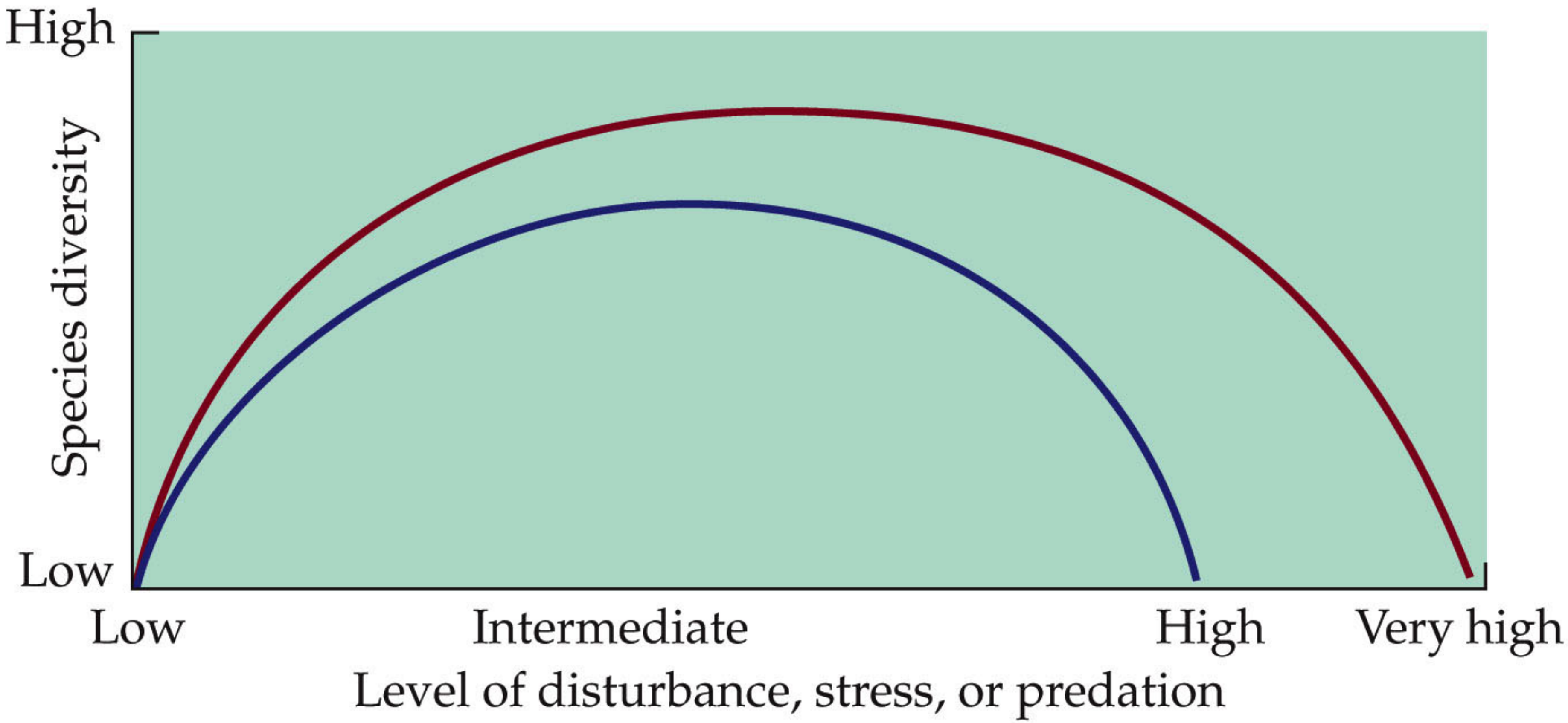
Resource Partitioning

Two diatom species were grown in media with different SiO_2:PO_4 ratios.

Tillman found that *Cyclotella* dominated only when the ratio was low, *Asterionella* dominated when the ratio was high.

Coexistence occurred only when SiO_2 and PO_4 were limiting to both species.

Figure 18.10 Resource Ratio Hypothesis



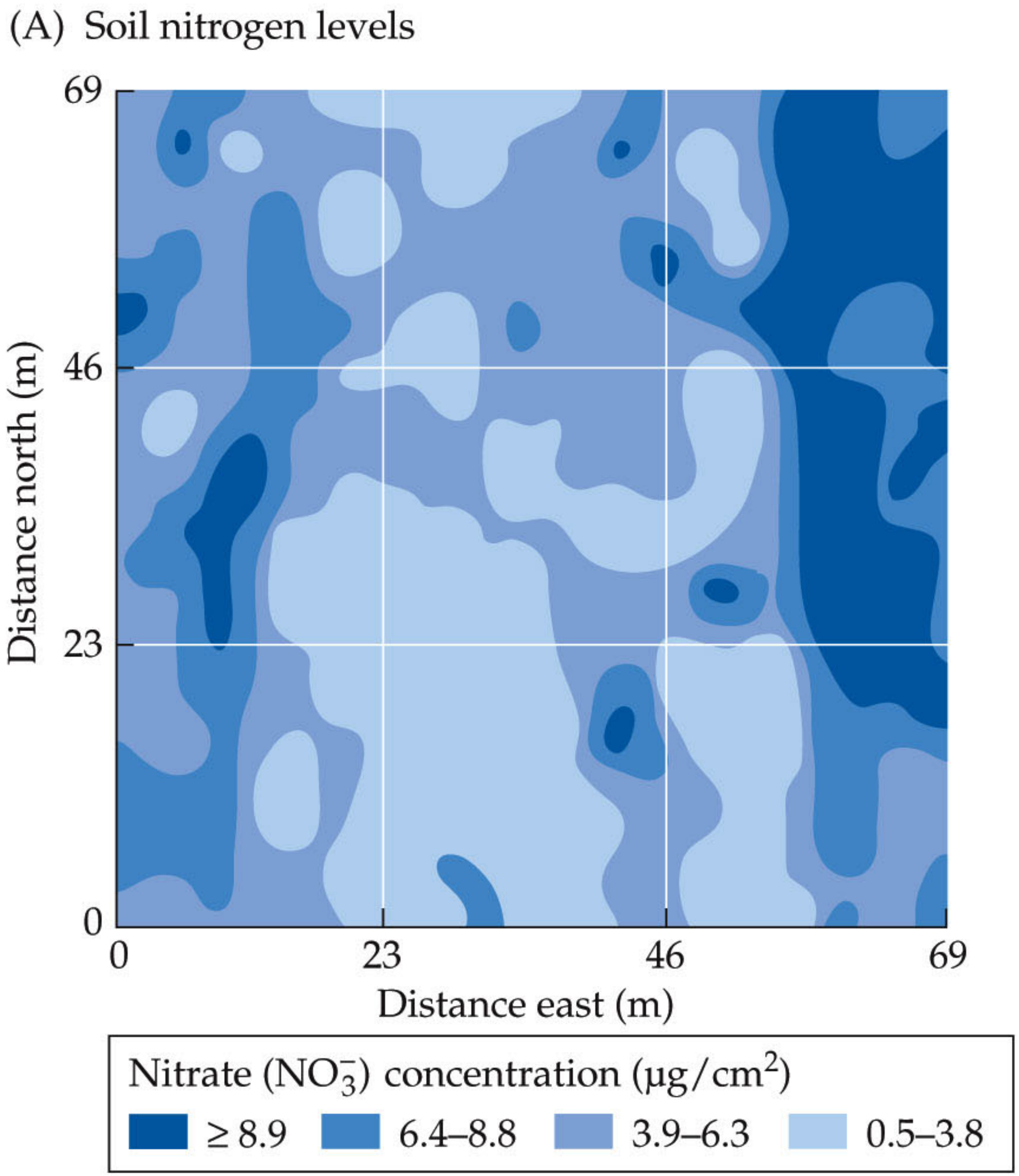
Resource Partitioning

In a field study, Robertson et al. (1988) mapped soil moisture and nitrogen concentration and found considerable variation over small spatial scales.

If the two maps are combined, patches corresponding to different proportions of these two resources emerge.

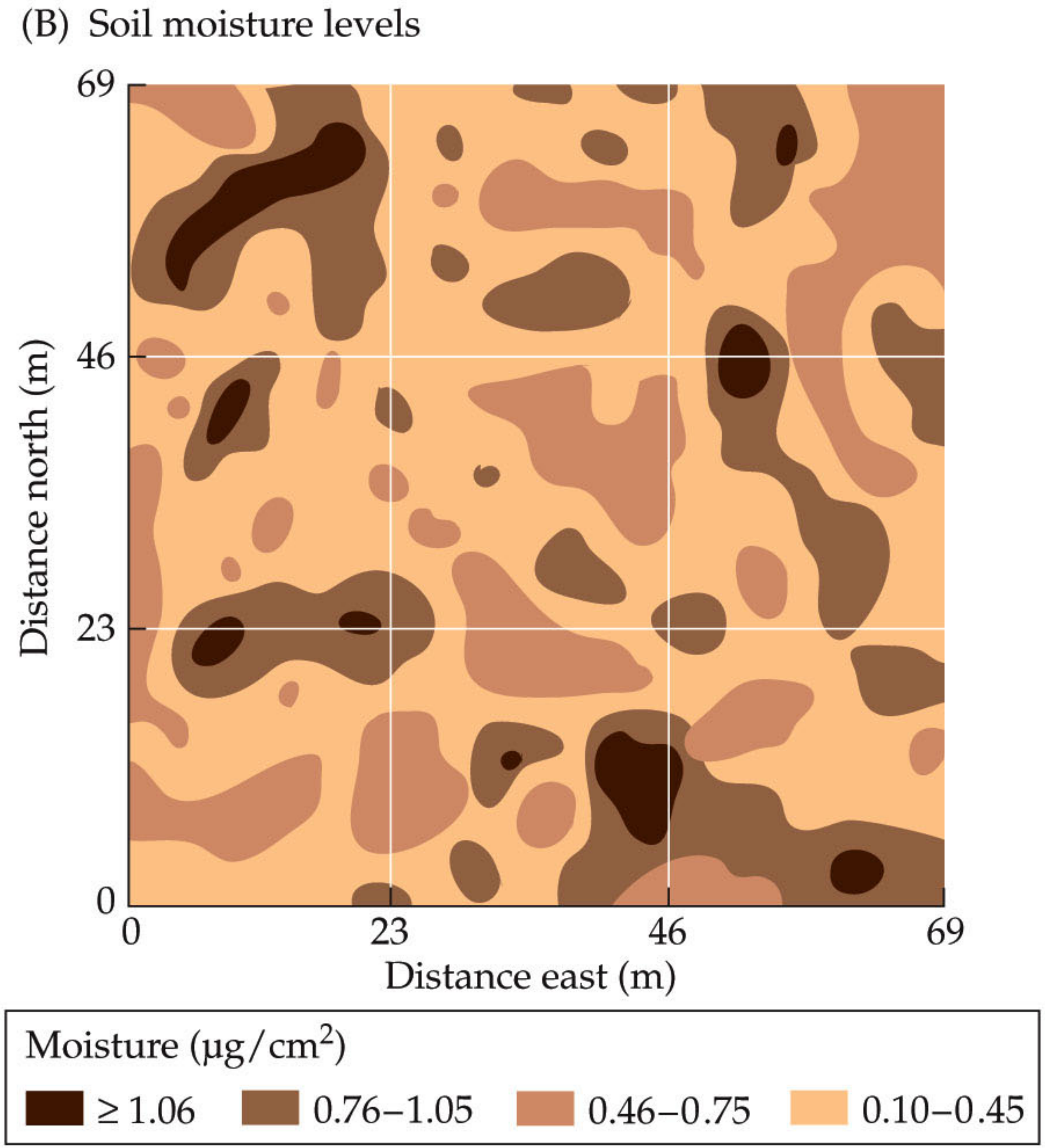
This suggests that resource partitioning could occur in plants.

Figure 18.11 Resource Distribution Maps (Part 1)



ECOLOGY, Figure 18.11 (Part 1)

Figure 18.11 Resource Distribution Maps (Part 2)



ECOLOGY, Figure 18.11 (Part 2)

Resource Partitioning

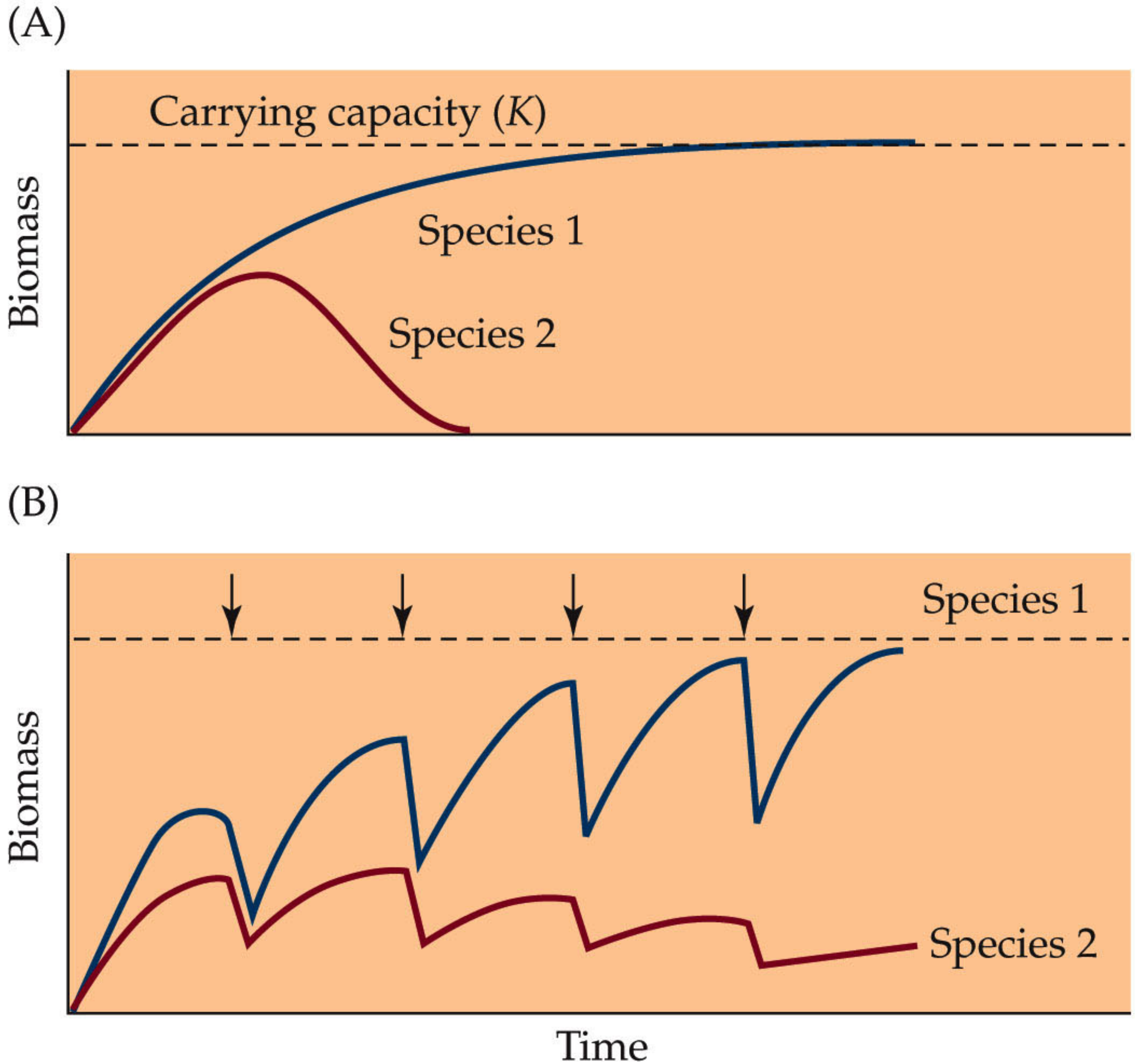
The theory of resource partitioning assumes that species have reached a stable population size (carrying capacity) and that resources are limiting.

Some ecologists have argued that this assumption is unrealistic because species' populations fluctuate in space and time.

Concept 18.3: Nonequilbrium processes such as disturbance, stress, and predation can mediate resource availability, thus affecting species interactions and coexistence.

When the dominant competitor is unable to reach its own carrying capacity because disturbance, stress, or predation, competitive exclusion can’t occur, and coexistence will be maintained.

Figure 18.12 The Outcome of Competition under Equilibrium versus Nonequilibrium Conditions



ECOLOGY, Figure 18.12

Nonequilibrium Theories

Darwin first considered disturbance as a mechanism to maintain species diversity.

In a meadow that he stopped mowing, he observed that the species number went from 20 down to 11.

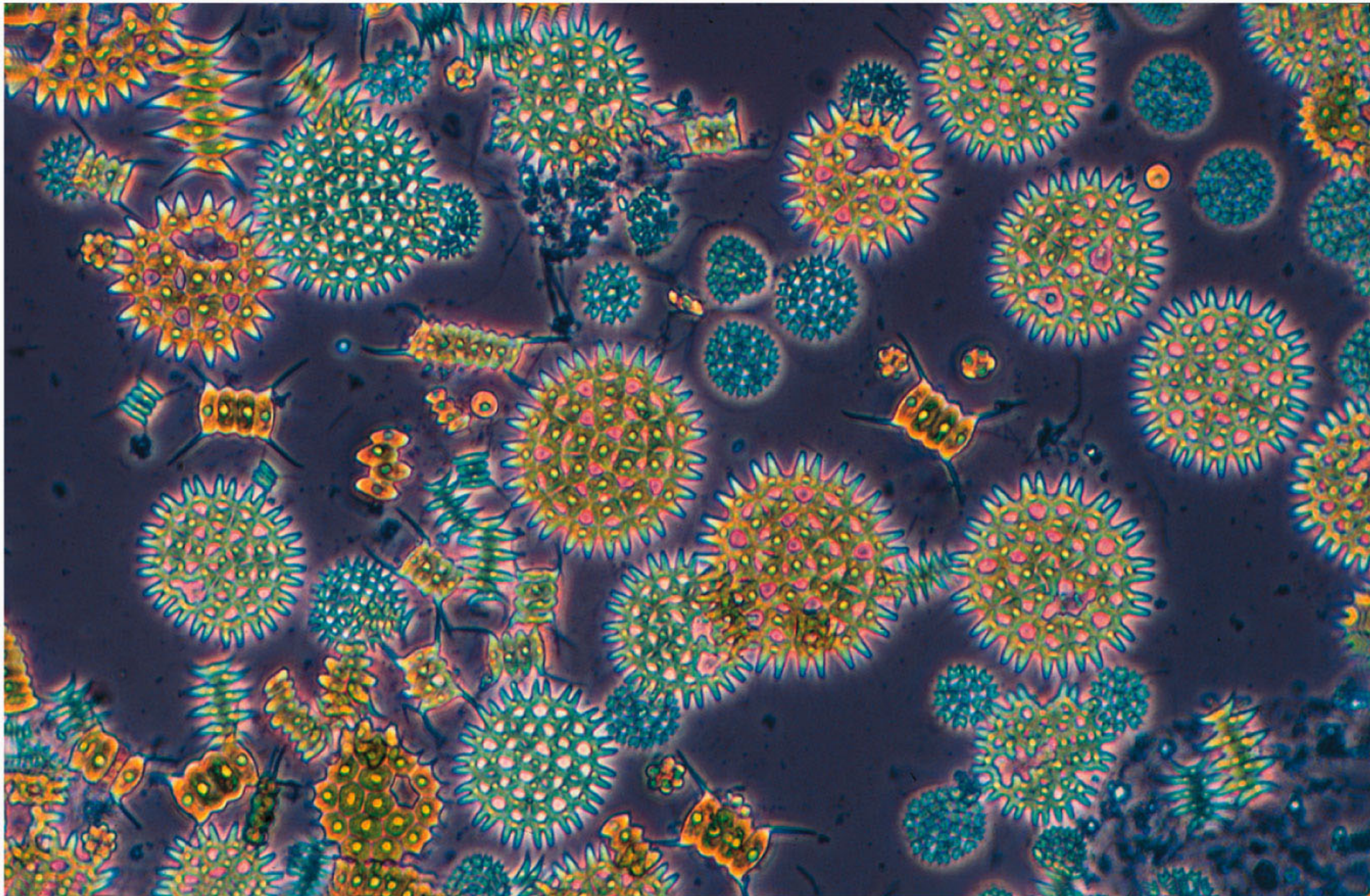
With no disturbance (mowing), the dominant species were able to exclude several others.

Nonequilibrium Theories

G. E. Hutchinson considered the nonequilibrium theory with his paper “The Paradox of the Plankton” (1961).

He observed that phytoplankton communities in freshwater lakes had very high diversity (30–40 species) despite the apparently limited amount of resources and homogeneous environment.

Figure 18.13 Paradox of the Plankton



Nonequilibrium Theories

He reasoned that all phytoplankton species compete for the same resources, such as CO_2, P, N, etc. that are likely to be evenly distributed in the lake water.

His explanation was that conditions in the lake changed seasonally, which kept any one species from outcompeting the others.

Nonequilibrium Theories

As long as conditions in the lake changed before competitively superior species reached carrying capacity, coexistence would be possible.

Hutchinson's model has two components:

Time required for one species to exclude another (t_c), which depends on the population growth rates of the two species.

Time it takes environmental variation to act on population growth of the two species (t_e).

Nonequilibrium Theories

If $t_c \ll t_e$, coexistence cannot be achieved.

This could occur in environments with little variability, or if the dominant species had very fast growth rates.

In a fluctuating environment, $t_c \gg t_e$, competitive exclusion can occur.

Nonequilibrium Theories

Coexistence can only occur when $t_c = t_e$.

This condition is likely to be met frequently in lake phytoplankton communities.

Robert Paine (1966) studied competitive exclusion in the rocky intertidal zone.

He manipulated population densities of a predator (the sea star *Pisaster*) which feeds preferentially on the mussel *Mytilus californianus*.

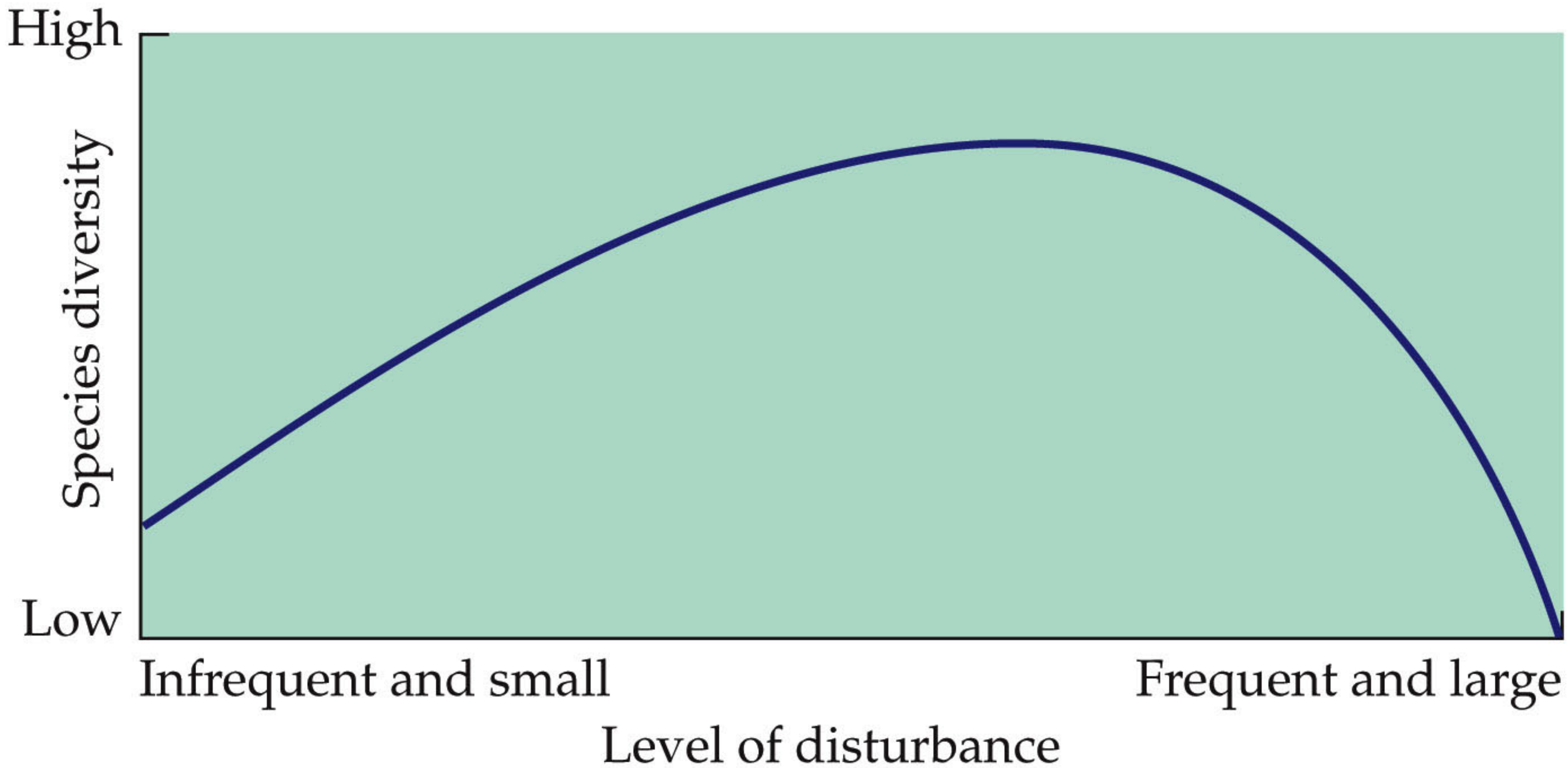
When *Pisaster* was present, diversity was higher. Without *Pisaster*, *Mytilus* outcompeted other species.

Nonequilibrium Theories

Paine’s work stimulated research on the **intermediate disturbance hypothesis**, first proposed by Connell (1978):

Species diversity should be highest at intermediate levels of disturbance.

At low levels of disturbance, competition would determine diversity. At high disturbance levels, many species would not be able to survive.


High
Low
Species diversity
Infrequent and small
Frequent and large
Level of disturbance

Nonequilibrium Theories

There have been many tests of this hypothesis.

Sousa studied communities on intertidal boulders in southern California.

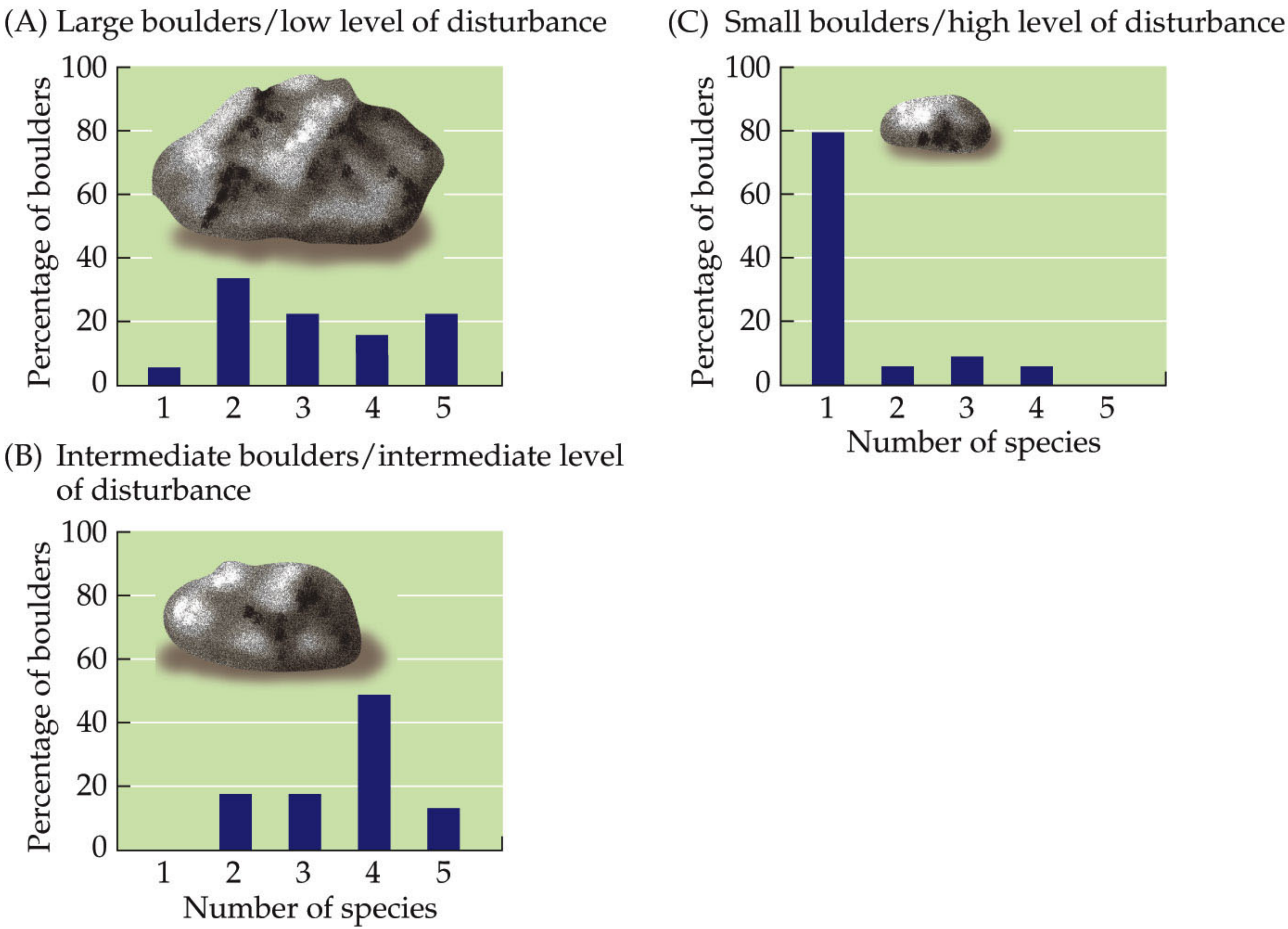
The frequency of boulders being overturned by waves was determined by size of boulders. Thus, small boulders underwent disturbance frequently, large boulders much less often.

Nonequilibrium Theories

Intermediate-sized boulders were rolled over at intermediate frequencies.

After 2 years, most small boulders had one species living on them; most large boulders had two species, and intermediate sized boulders had four to seven species.

Figure 18.15 A Test of the Intermediate Disturbance Hypothesis



Nonequilibrium Theories

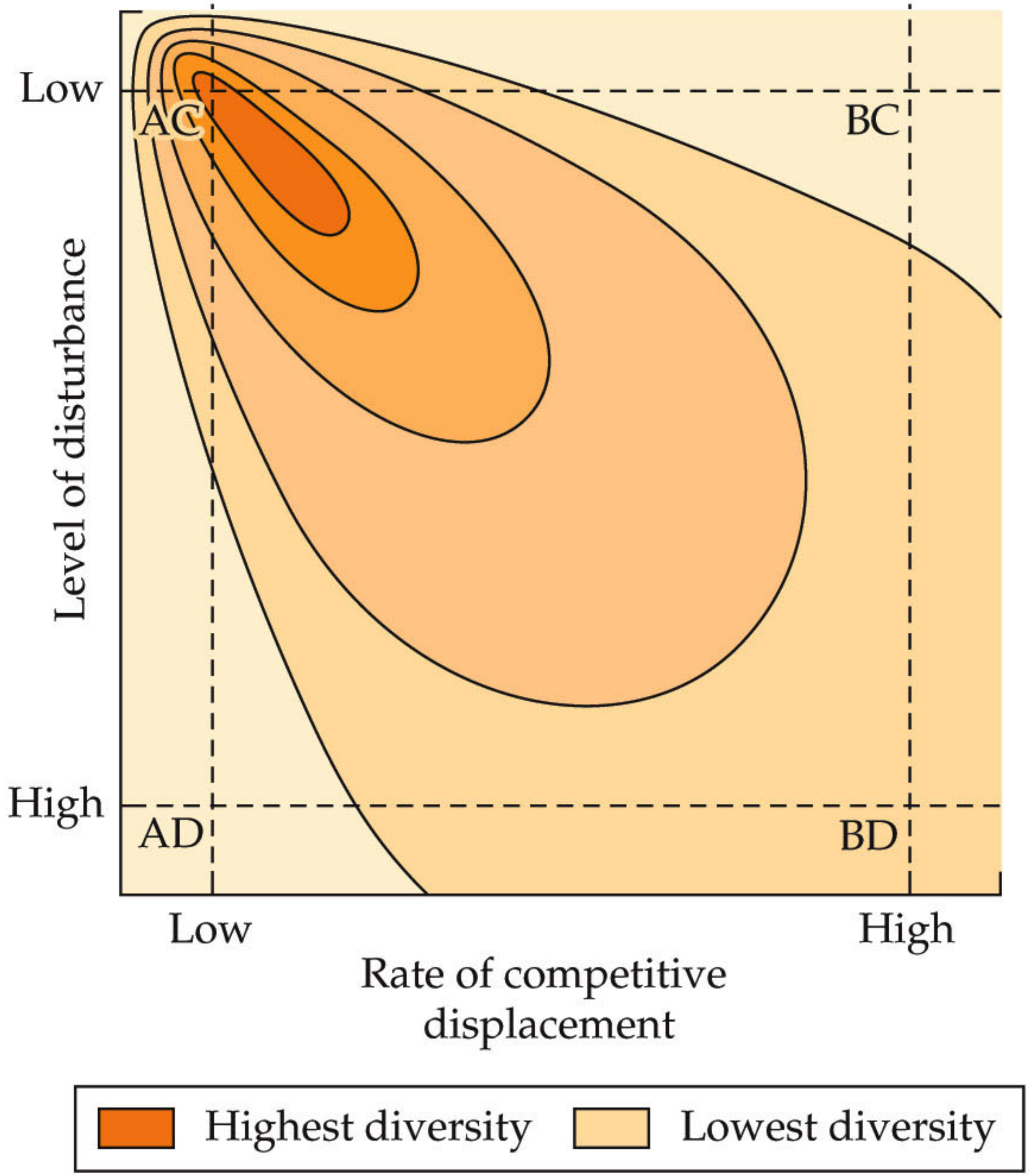
Huston (1979) added **competitive displacement**—the growth rate of the strongest competitors in a community. It is dependent on the productivity of the community.

His **dynamic equilibrium model** considers how disturbance frequency and the rate of competitive displacement combine to determine species diversity.

Nonequilibrium Theories

The model predicts maximum species diversity when the level of disturbance and the rate of competitive displacement are equal, and are at intermediate levels.

Figure 18.16 The Dynamic Equilibrium Model



Nonequilibrium Theories

There have been only a few tests of this model.

Pollock et al. (1998) surveyed riparian wetlands of different types in Alaska.

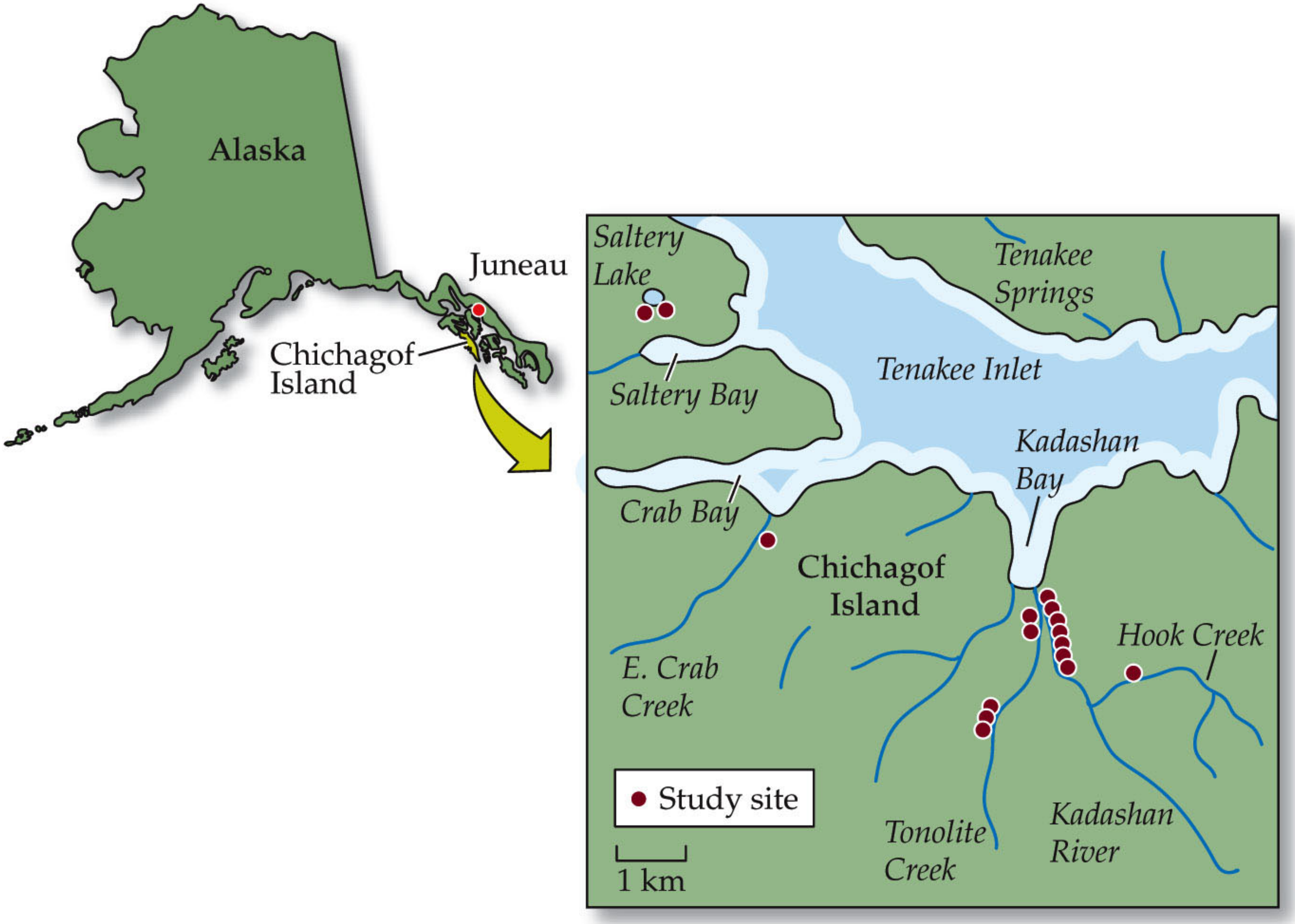
The sites varied in flood frequency (level of disturbance) and productivity (rate of competitive displacement).

Nonequilibrium Theories

Plant species richness roughly followed the dynamic equilibrium model.

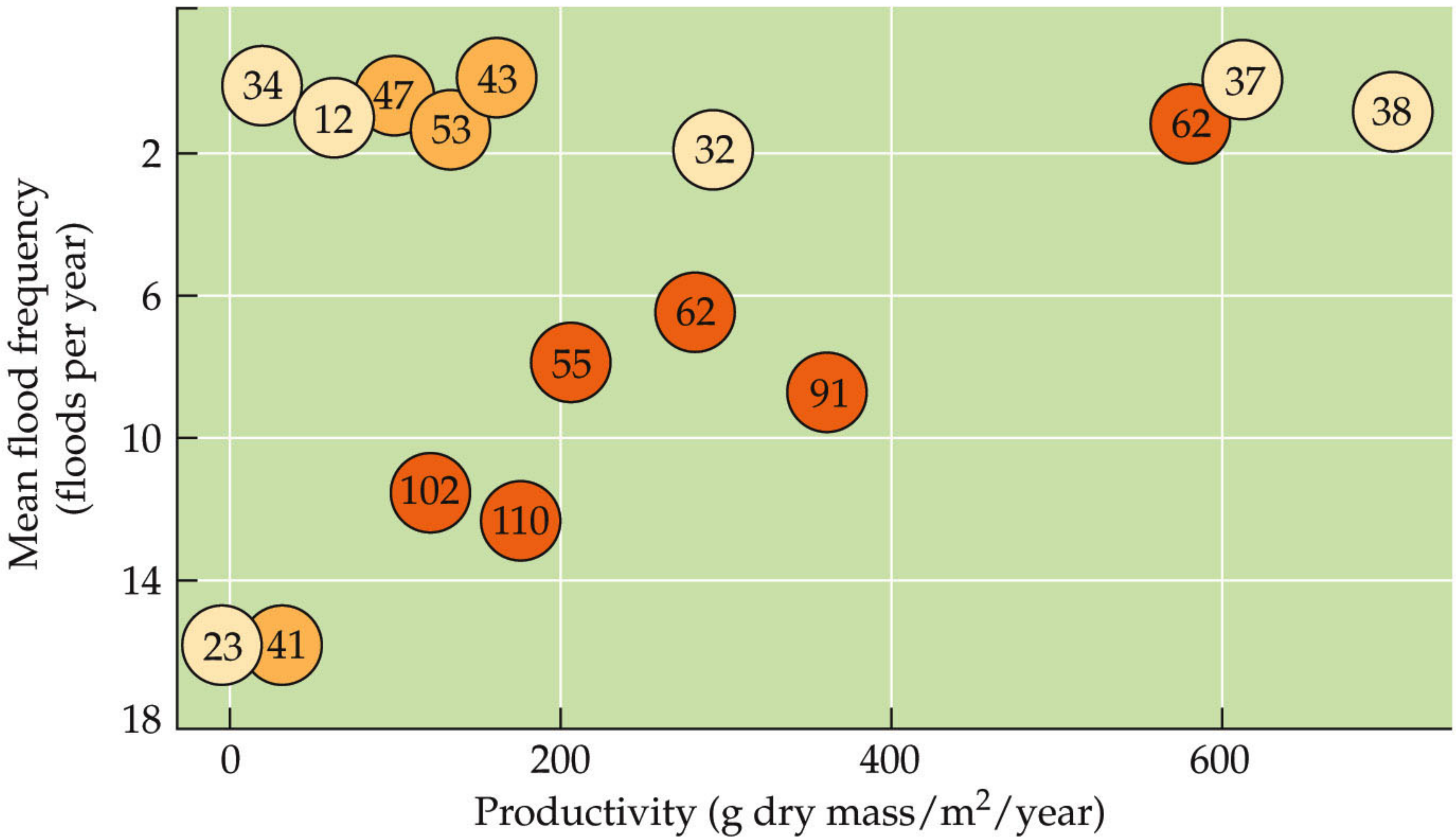
- Species-poor sites had very low or very high flood frequencies and low productivity.
- 78% of the observed variation in plant species richness could be attributed to disturbance and productivity.

Figure 18.17 The Dynamic Equilibrium Model in Alaskan Wetlands (Part 1)



ECOLOGY, Figure 18.17 (Part 1)

Figure 18.17 The Dynamic Equilibrium Model in Alaskan Wetlands (Part 2)



Nonequilibrium Theories

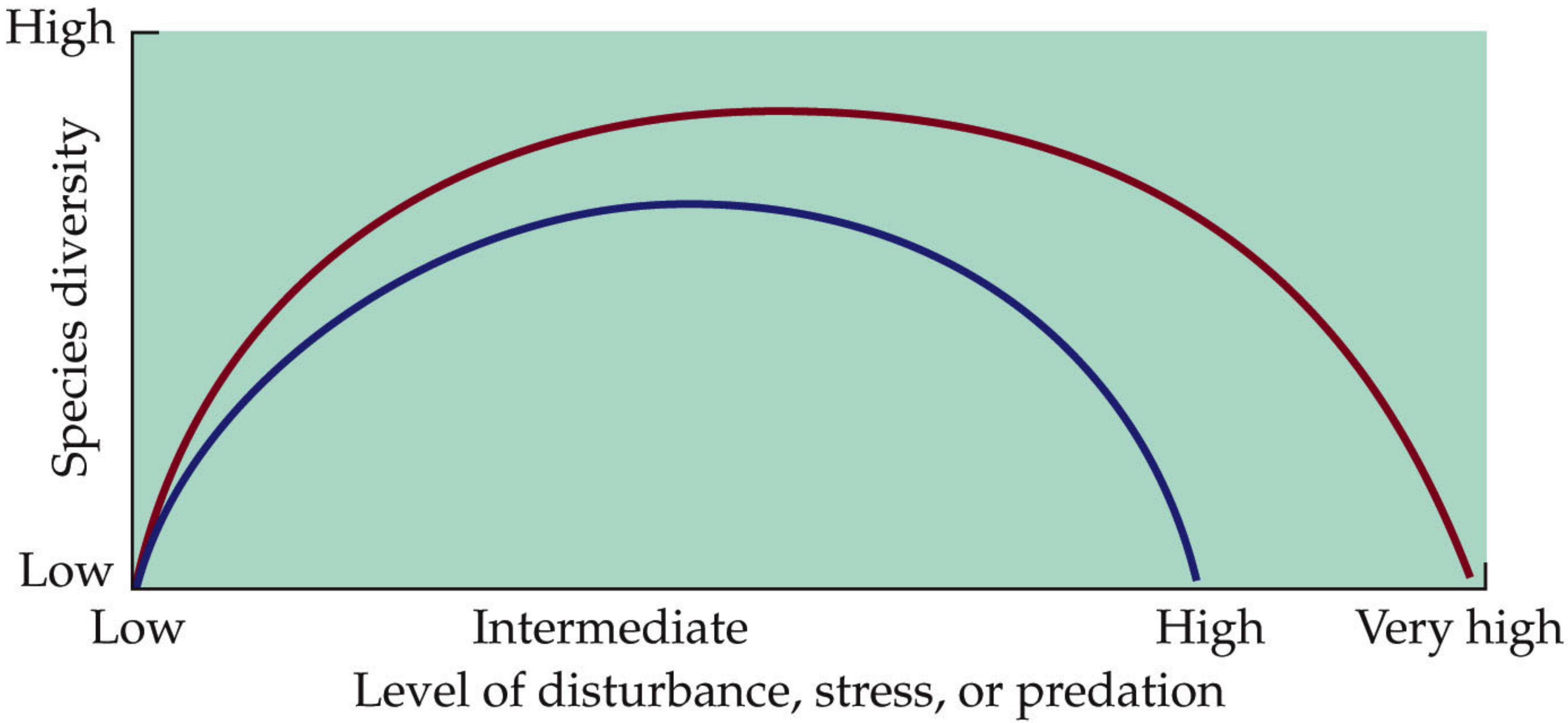
Hacker and Gaines (1997) incorporated positive interactions into the intermediate disturbance hypothesis.

Evidence suggests that positive interactions are more common under relatively high levels of disturbance, stress, or predation.

Nonequilibrium Theories

- At low levels of disturbance, competition reduces diversity.
- At intermediate levels, species that have positive effects are released from competition and can increase diversity.
- At high levels, positive interactions are common and help to increase diversity.

Figure 18.18 Positive Interactions and Species Diversity



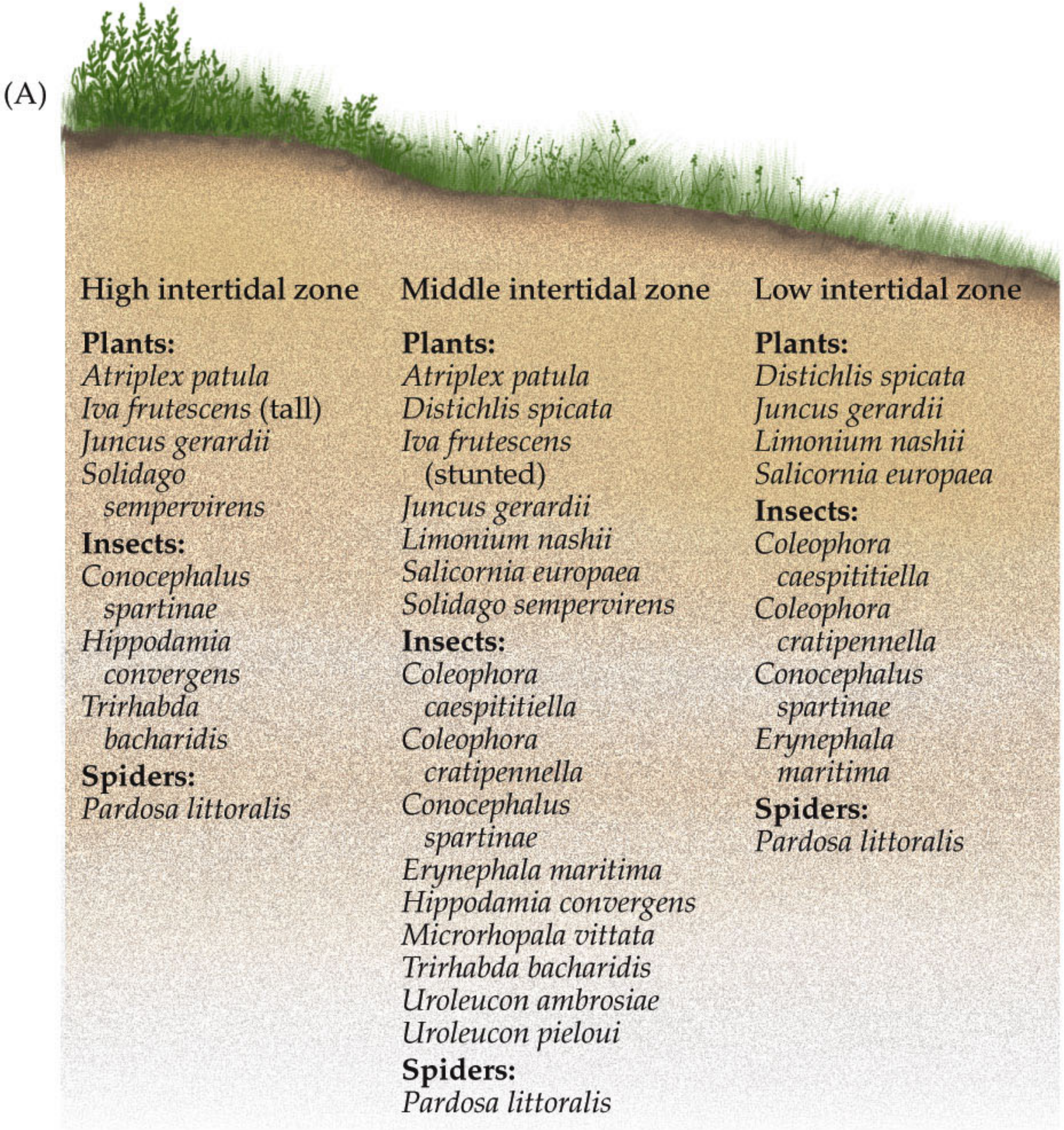
Nonequilibrium Theories

A New England salt marsh case study was used to support their idea.

Highest stress occurs closest to the shoreline, and close to the terrestrial border.

Three distinct zones result. The middle intertidal zone had greatest species richness.

Figure 18.19 A Positive Interactions: Key to Local Diversity in Salt Marshes?



ECOLOGY, Figure 18.19 (Part 1)

Transplant experiments showed that competition with *Iva* in the high intertidal zone led to the competitive exclusion of most plant species transplanted there.

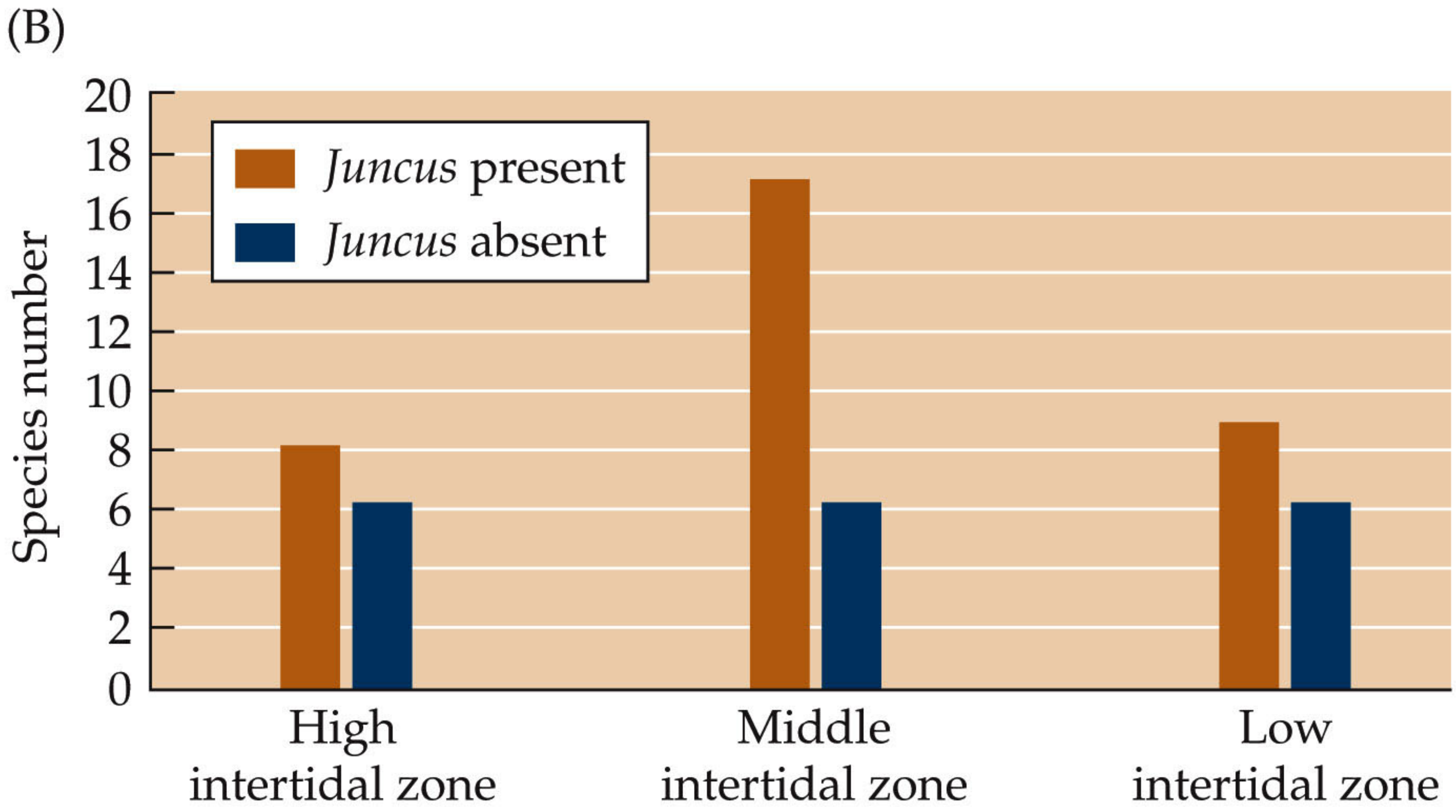
In the low intertidal zone, physiological stress was the main controlling factor; many individuals died whether *Juncus* was present or absent.

Nonequilibrium Theories

In the middle intertidal zone, *Juncus* facilitated other plant species. Without *Juncus*, most species died.

Facilitation included reduction of salt stress and hypoxia by *Juncus.* Many herbivores were also indirectly facilitated.

Figure 18.19 B Positive Interactions: Key to Local Diversity in Salt Marshes?



Researchers concluded that positive interactions were critically important in maintaining species diversity, especially at the intermediate stress levels of the middle intertidal zone.

Physical stress in the middle intertidal zone both decreases the competitive effect of *Iva* and increases the facilitative effect of *Juncus.*

Nonequilibrium Theories

The above theories assume an underlying competitive hierarchy.

What if species have equivalent interaction strengths?

The **lottery model** emphasizes the role of chance. It assumes that resources are captured at random by recruits from a larger pool of potential colonists.

Nonequilibrium Theories

In this model, species must have similar interaction strengths and population growth rates, and the ability to disperse quickly to disturbances that free up resources.

All species have equal chances of obtaining resources, which allows coexistence.

Nonequilibrium Theories

A survey of fish diversity on the Great Barrier Reef shows extremely high diversity, even in small patches.

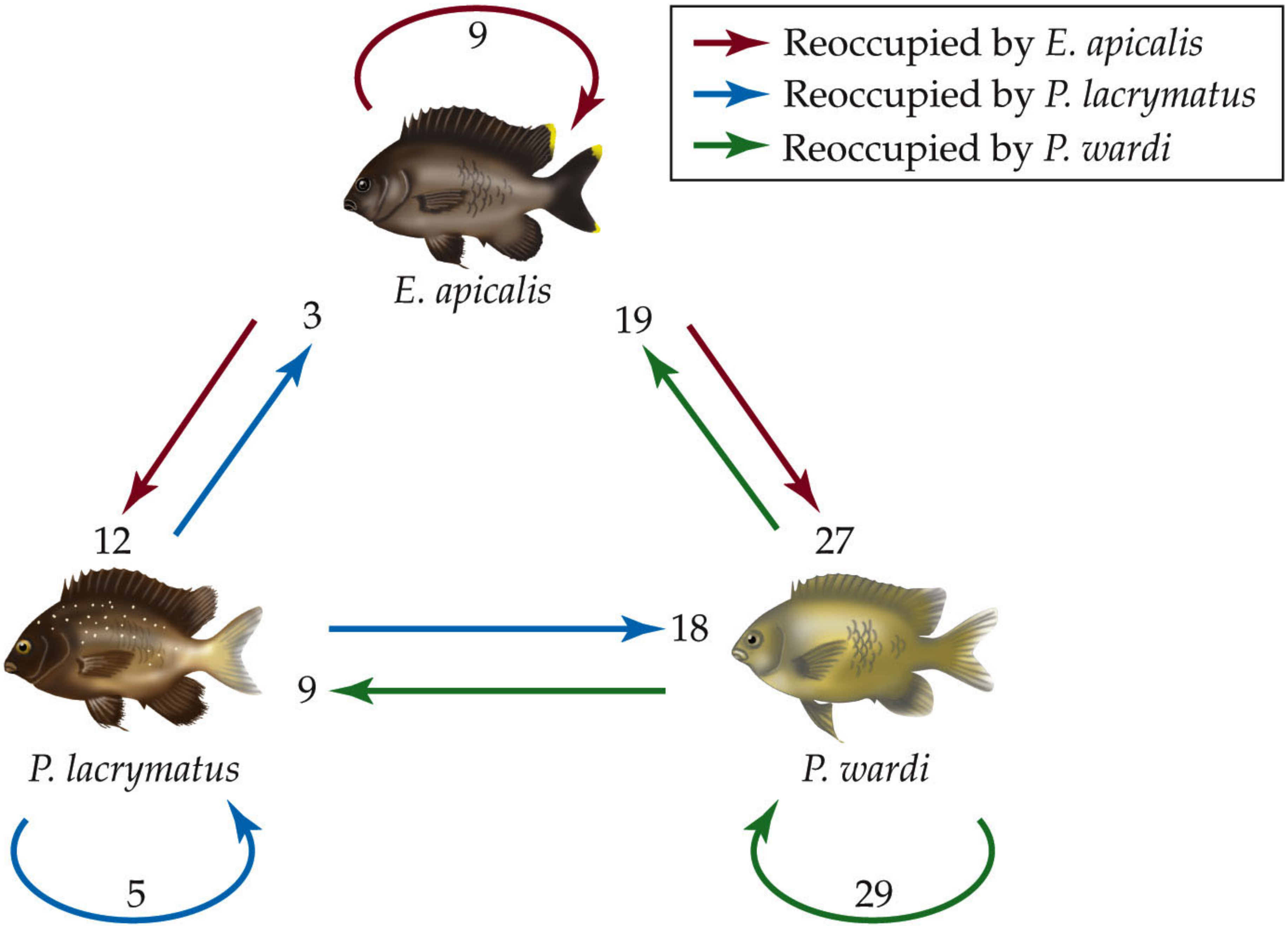
Many species have very similar diets, making resource partitioning unlikely.

New territories open unexpectedly after deaths of occupants—by predation, etc.

Nonequilibrium Theories

Sale (1977) looked at patterns of occupation of new sites by three fish species, and found it to be random.

One important component of this lottery system was that fishes produce many highly mobile juveniles that can saturate a reef and quickly take advantage of open space.



ECOLOGY, Figure 18.20 (Part 1)

This mechanism might be particularly relevant in very diverse communities where so many species overlap in their resource requirements.

Its relevance decreases in communities in which species have large disparities in interaction strength.

Concept 18.4: Experiments show that species diversity is positively related to community function.

A central idea in ecology is that species diversity can control certain functions in a community, such as primary productivity, soil fertility, resistance to disturbance, and speed of recovery (**resilience**).

Many of these functions also provide valuable services to humans: Food and fuel production, water purification, O_2 and CO_2 exchange, and protection from catastrophic events, such as floods.

The Millennium Ecosystem Assessment (2005) predicts that if the current losses of species diversity continue, the world's human populations will be severely affected.

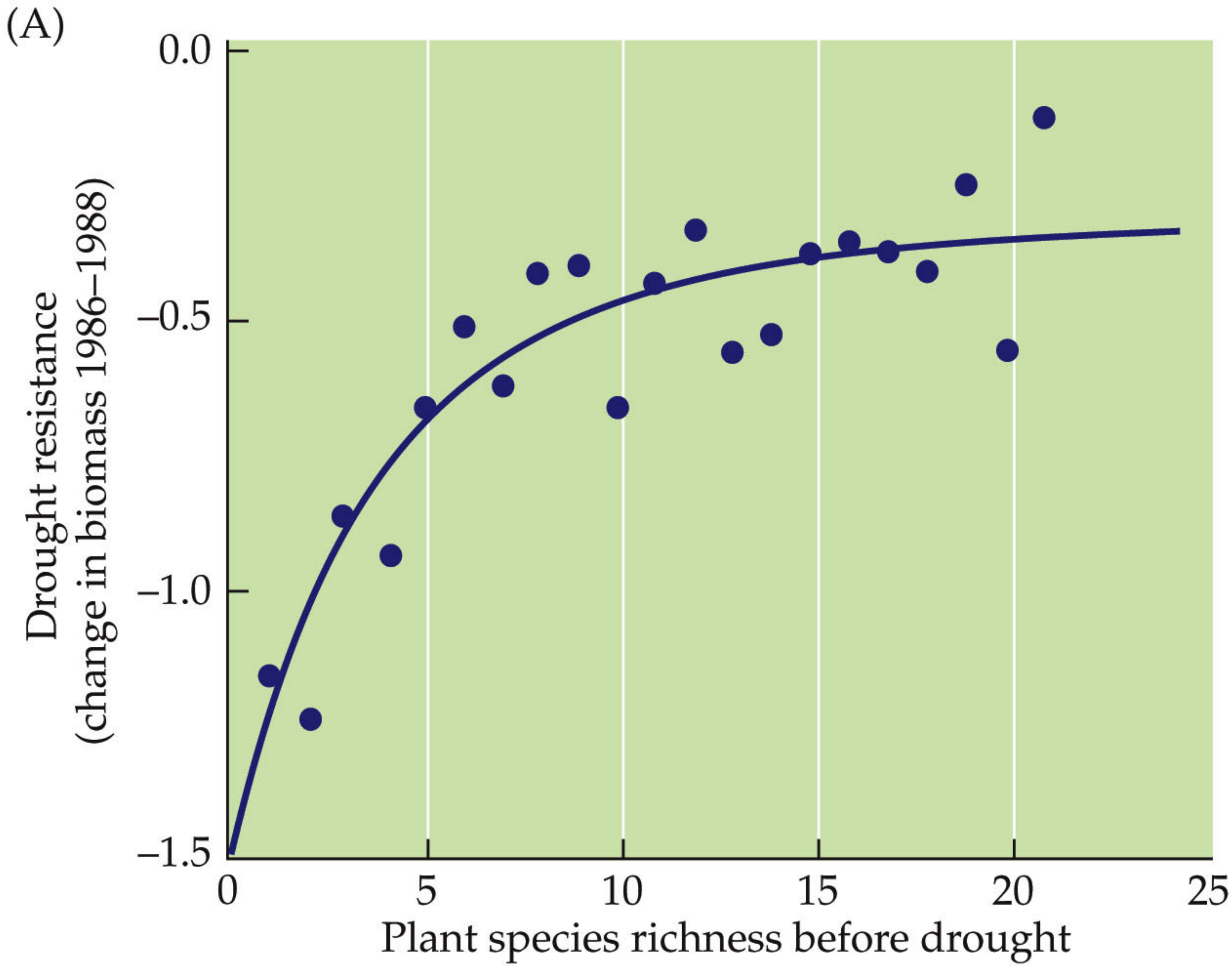
The Consequences of Diversity

A long-standing idea in ecology is that species richness is positively related to community **stability**—the tendency of a community to remain the same in structure and function.

The Consequences of Diversity

Tilman and Downing (1994), working in the experimental plots at Cedar Creek, showed that plots with higher species richness (but equal density) had better drought resistance than plots with lower species richness.

Figure 18.21 A Species Diversity and Community Function

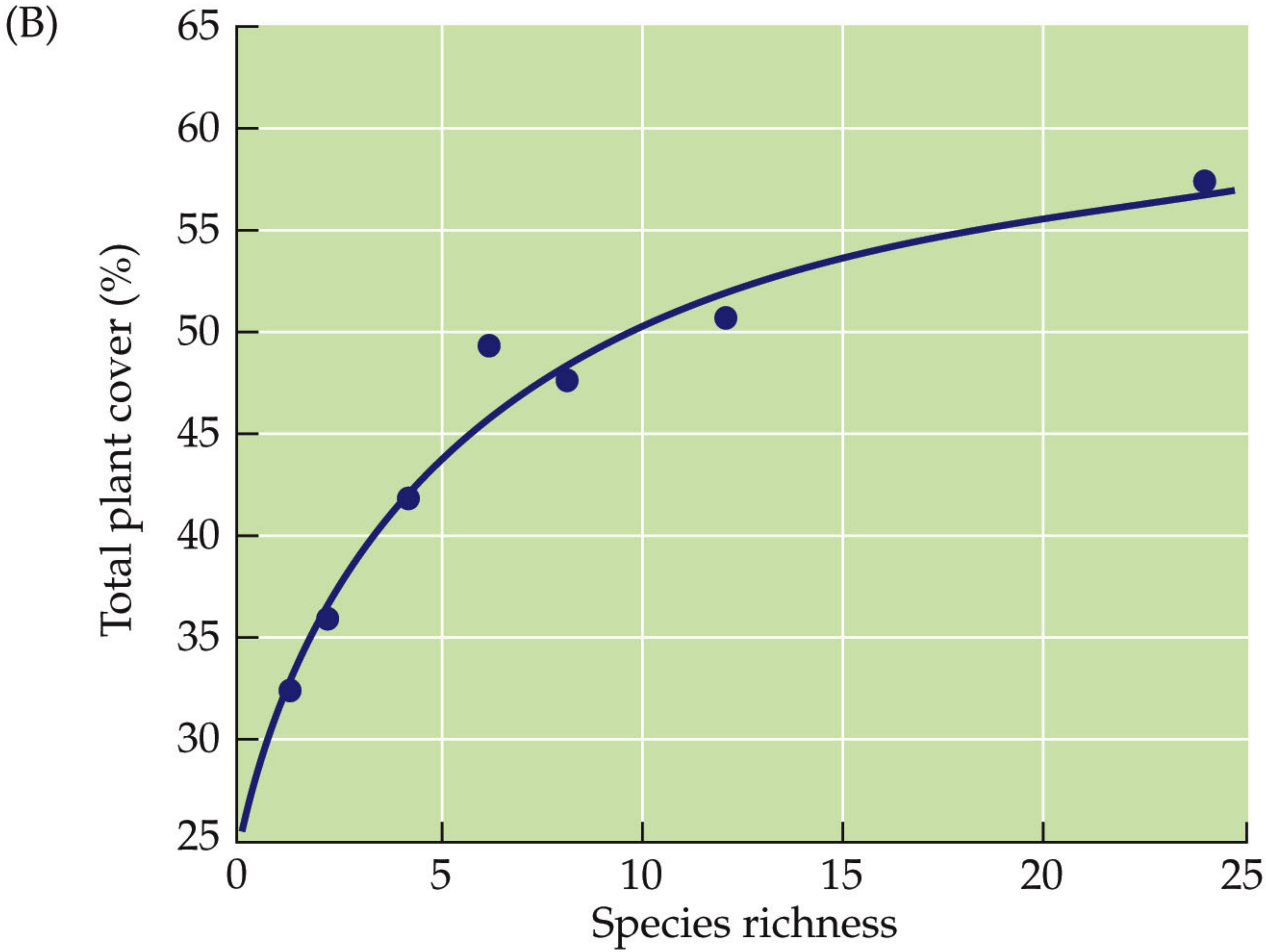


ECOLOGY, Figure 18.21 (Part 1)

A curvilinear relationship would be expected if additional species beyond some threshold had little additional effect on drought resistance.

They tested this with another experiment. Using a pool of 24 species, they set up plots with different numbers of species, but the same number of individuals.

Figure 18.21 B Species Diversity and Community Function

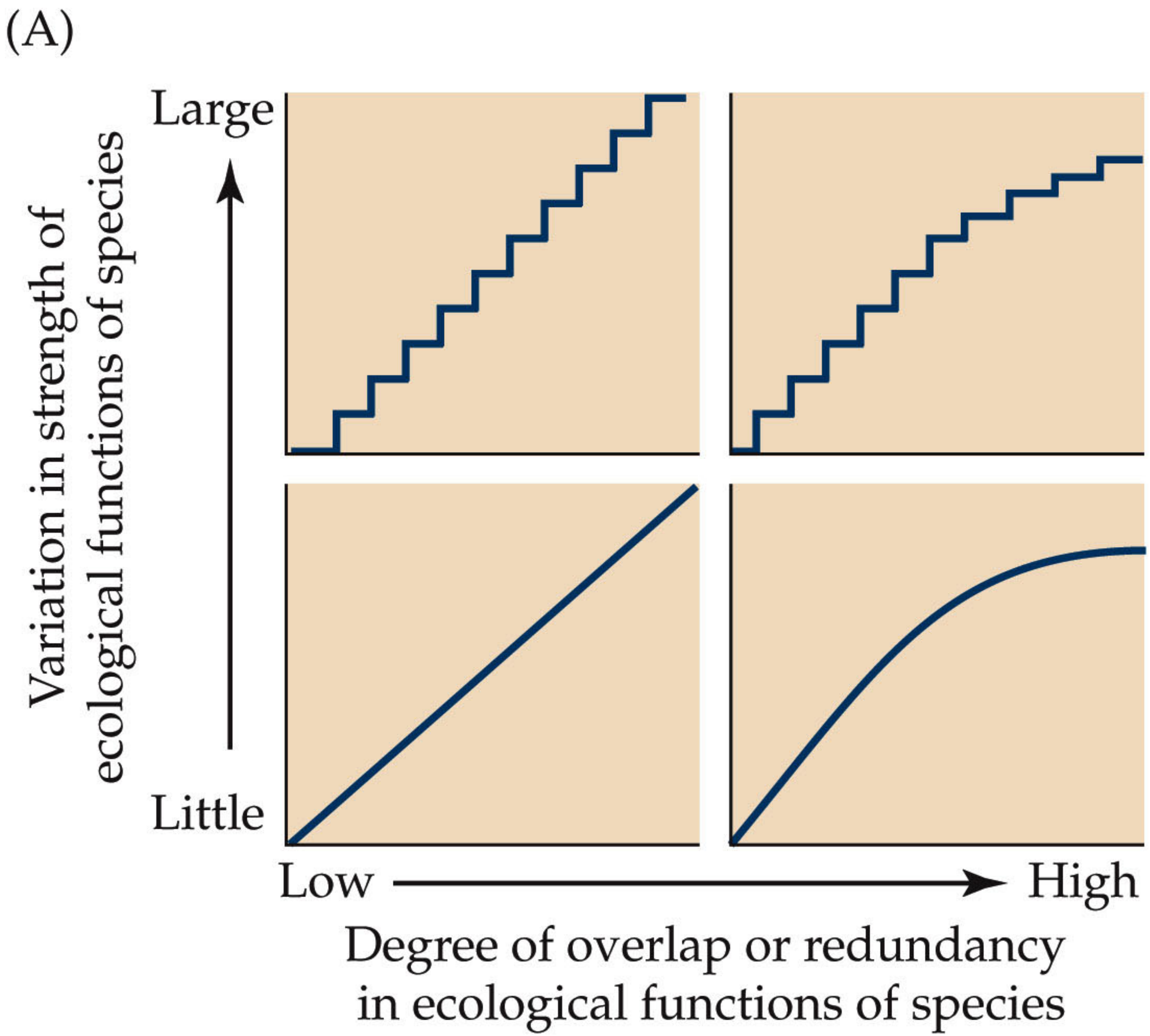


ECOLOGY, Figure 18.21 (Part 2)

There are at least four hypotheses on the mechanisms that underlie these relationships.

Two variables in all the hypotheses are the degree of overlap in the ecological function of species, and variation in the strength of the ecological functions of species.

Figure 18.22 A Hypotheses on Species Richness and Community Function



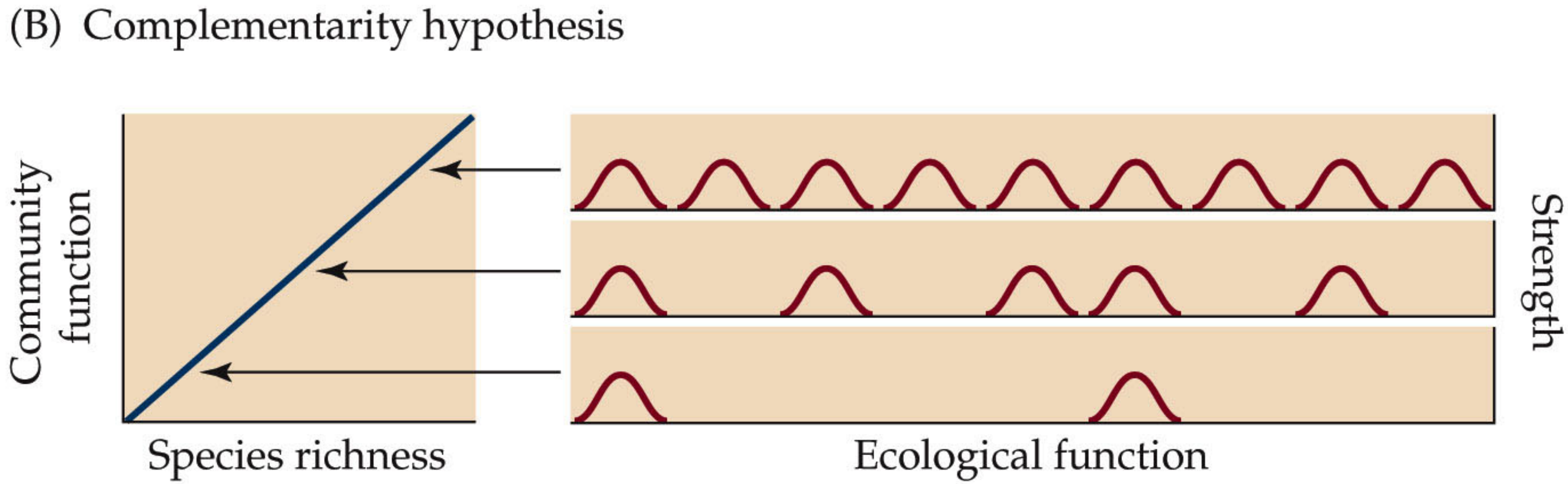
ECOLOGY, Figure 18.22 (Part 1)

1. **Complementarity hypothesis**:

As species richness increases, there will be a linear increase in community function.

Each species added has an equal effect.

Figure 18.22 B Hypotheses on Species Richness and Community Function

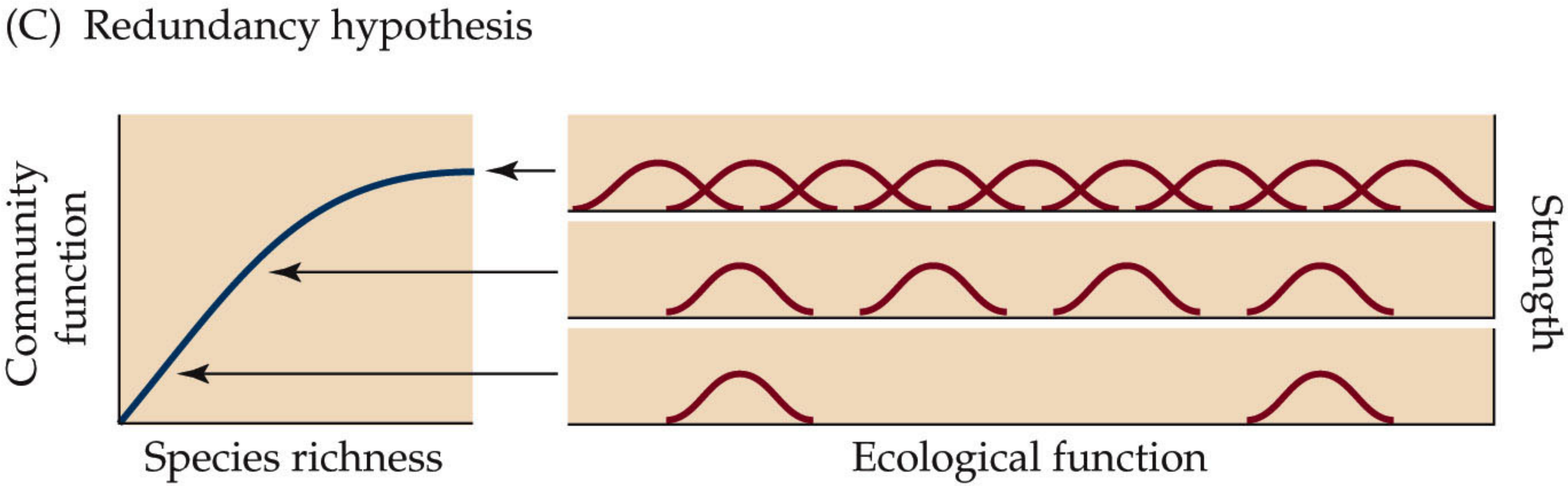


2. **Redundancy hypothesis**: The functional contribution of additional species reaches a threshold.

As more species are added, there is overlap in their function, or redundancy among species.

If species represent functional groups, and all the important groups are present, the actual species composition doesn't matter.

Figure 18.22 C Hypotheses on Species Richness and Community Function



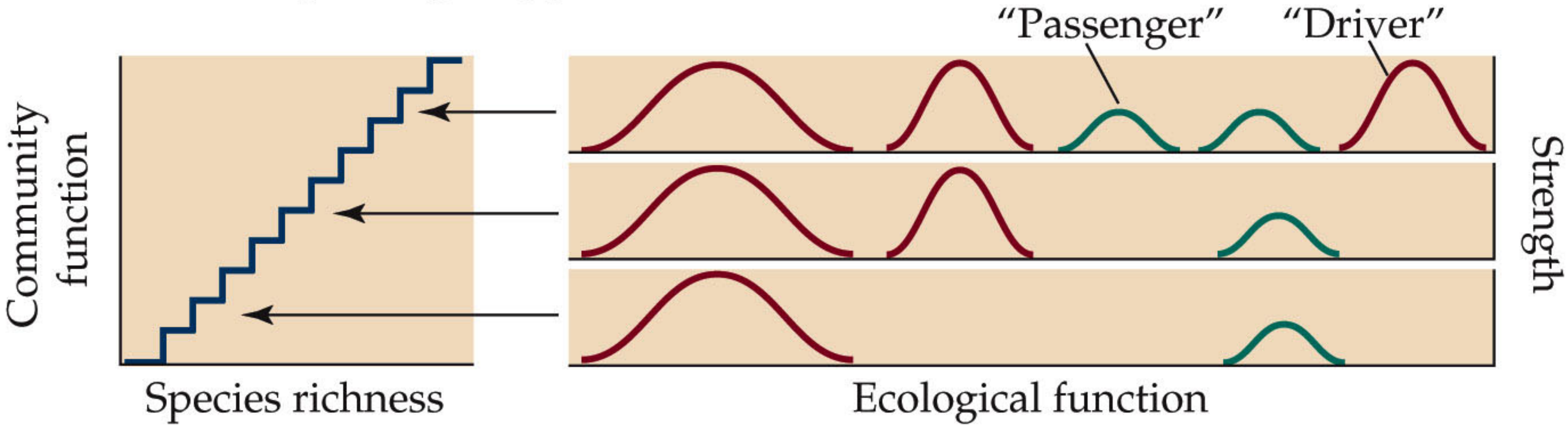
3. **Driver and passenger hypothesis**:

Strength of ecological function varies greatly among species. “Driver” species have a large effect, “passenger” species have a minimal effect.

Addition of driver and passenger species to a community will therefore have unequal effects on community function.

Figure 18.22 D Hypotheses on Species Richness and Community Function

(D) Driver and passenger hypothesis

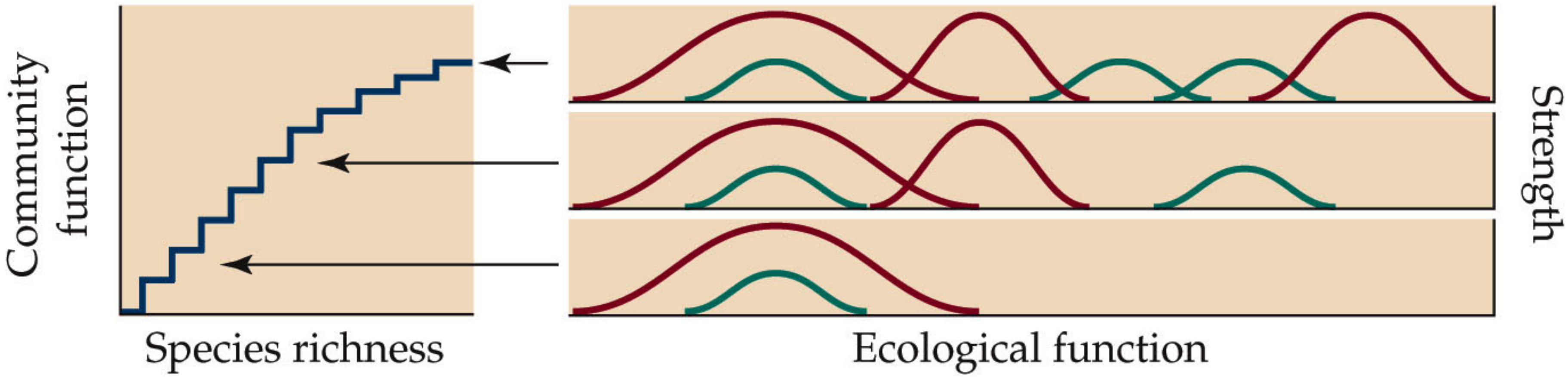


The Consequences of Diversity

4. A variation on the driver and passenger hypothesis:

It assumes there could be overlap between driver and passenger functions.

(E) Driver and passenger hypothesis with overlap



Experiments to test these hypotheses will be logistically challenging.

They can tell us something about how communities work.

They may be able to tell us what the future holds for communities that are both losing (by extinction) and gaining (by invasions) species through human influence.

Biodiversity and Biofuels

Tilman et al. (2006) showed that high-diversity plots produced nearly 238% more biomass per input of energy than single-species plots.

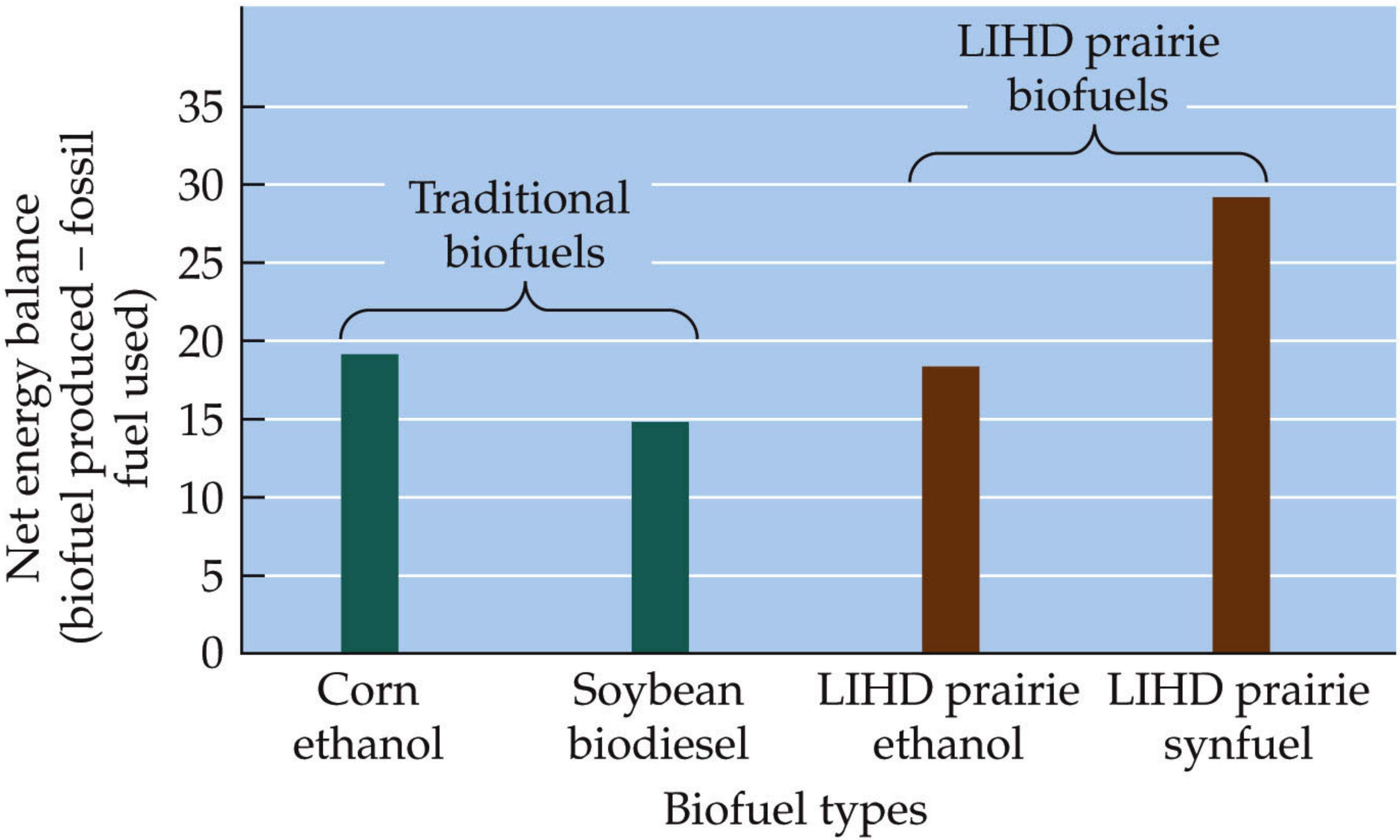
They looked at three types of biomass that could be used for biofuels—soybeans, corn, and low-input, high-diversity (LIHD) biomass from their prairie plots.

Case Study Revisited: Powered by Prairies? Biodiversity and Biofuels

Three types of fuels, biodiesel, ethanol, and synfuel (synthetic gasoline), can be made from these crops.

Synfuel from LIHD prairie biomass had the highest net energy balance (amount of biofuel produced minus the amount of fossil fuels used to produce it).

Figure 18.23 Biofuel Comparisons



ECOLOGY, **Figure 18.23**

Energy inputs were lower for LIHD crops because they are perennial plants and require little water, fertilizer, or pesticides.

LIHD crops had a very high yield of biomass due to diversity effects; and all of the aboveground plant material can be used.

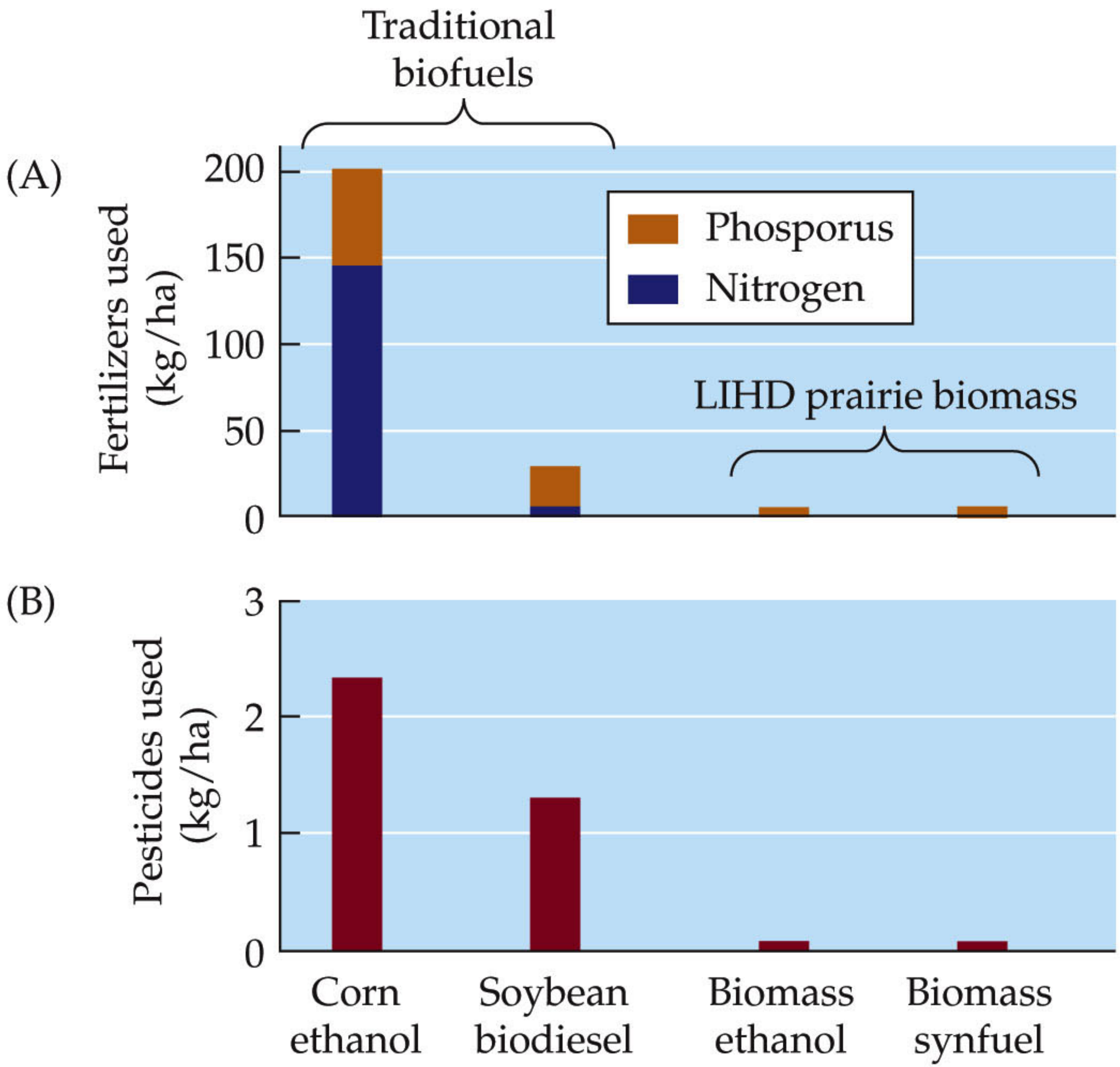
Case Study Revisited: Powered by Prairies? Biodiversity and Biofuels

Prairie plants also take up and store more CO_2 than corn and soybeans.

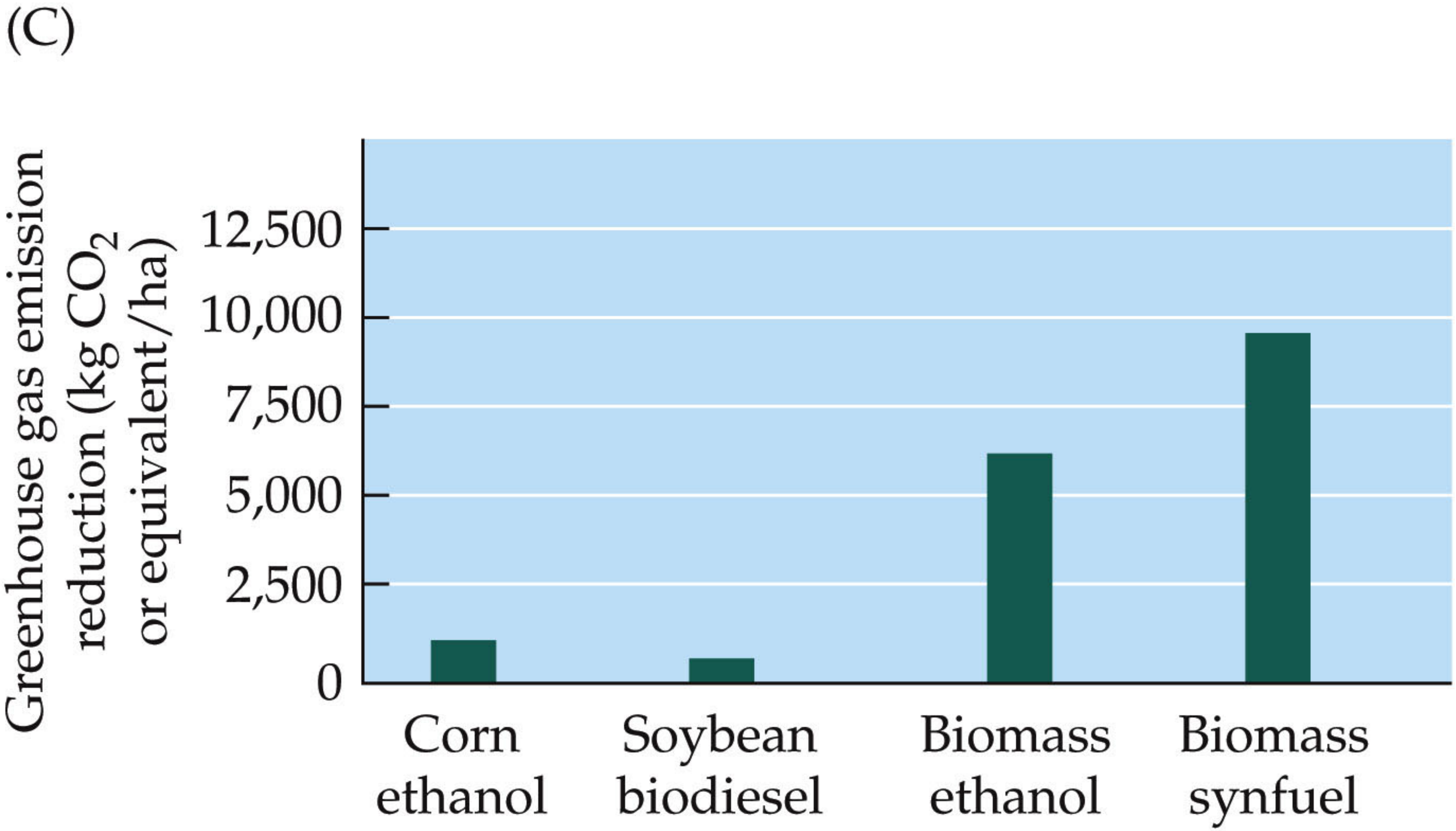
LIHD plots sequestered 160% more CO_2 in plant roots and soil than single-species prairie plots.

Greenhouse gas emission reductions relative to burning fossil fuels were 6 to 16 times greater for LIHD fuels than for corn ethanol or soybean biodiesel.

Figure 18.24 Environmental Effects of Biofuels (Part 1)



ECOLOGY, **Figure 18.24 (Part 1)**


(C)
Greenhouse gas emission reduction (kg CO_2 or equivalent/ha)
12,500
10,000
7,500
5,000
2,500
0
Corn ethanol
Soybean biodiesel
Biomass ethanol
Biomass synfuel

Connections in Nature: Barriers to Biofuels: The Plant Cell Wall Conundrum

Biofuels vary in the biomass needed to produce them and the energy required to refine them.

Biodiesel is easily produced from oils such as soybean oil, but growing the crops can increase soil erosion, requires large amounts of water, and competes with food crops.

Ethanol is commonly made from corn grains that are fermented and distilled.

The energy costs associated with growing the grain and producing the ethanol are high, so there is only a slight energy gain in ethanol production.

Connections in Nature: Barriers to Biofuels: The Plant Cell Wall Conundrum

It also competes with food crops.

An acre of corn produces about 440 gallons of ethanol.

This is 4–5 months of driving for the average individual in the U.S.

The same amount of corn could feed one person for 20–27 years.

Connections in Nature: Barriers to Biofuels: The Plant Cell Wall Conundrum

Non-food biomass, such as crop residues, logging wastes, and prairie plants, can be used to produce cellulosic ethanol.

Breaking down cellulose—the major component of plant cell walls—is extremely difficult and requires special enzymes.

Connections in Nature: Barriers to Biofuels: The Plant Cell Wall Conundrum

Molecular biologists are developing genetically engineered enzymes that work on the plant both externally and internally.

For biofuels to be a viable alternative to fossil fuels, ecologists and molecular biologists will have to work together to break down the barriers to biofuels that currently exist.