15

The Nature of Communities

- *Case Study*: "Killer Algae!"
- What Are Communities?
- Community Structure
- Interactions of Multiple Species
- *Case Study Revisited*
- *Connections in Nature*: Stopping Invasions Requires Commitment

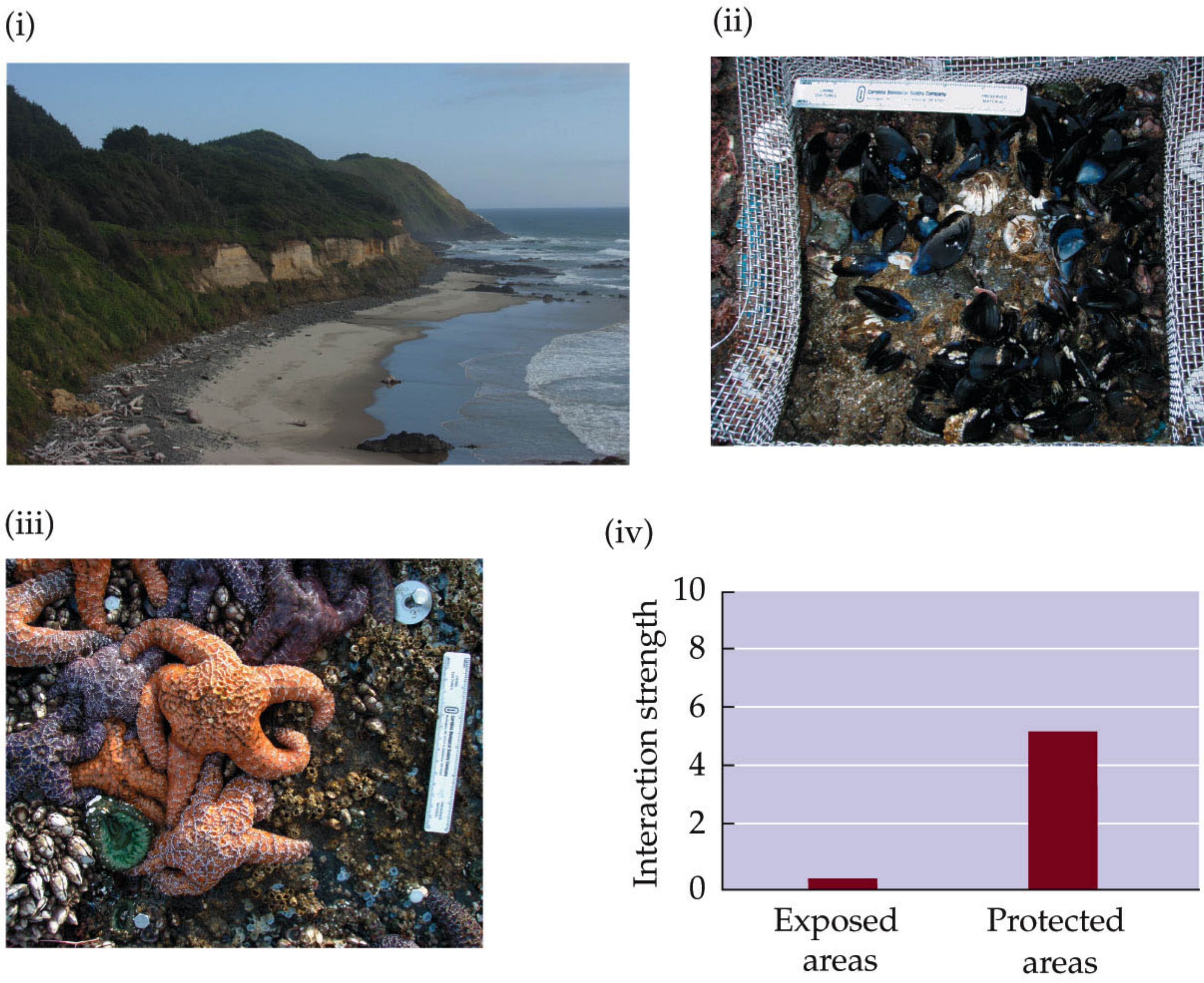
Case Study: “Killer Algae!”

In the 1980s, an unusual alga (*Caulerpa taxifolia)* was found in the Mediterranean Sea.

It was a native of warm Caribbean waters (18–20°C).

It had never been found in colder waters (12–13°C), nor in such densities. French marine biologists calculated its rate of spread at 1 hectare in 5 years.

Figure 15.1 Invading Algae



Case Study: “Killer Algae!”

Caulerpa produces secondary compounds that deter fish and invertebrate herbivores.

“Killer algae!” headlines implied it was toxic to humans, but it is not.

Caulerpa spread quickly.

Figure 15.2 Spread of *Caulerpa* in the Mediterranean Sea

ECOLOGY, Figure 15.2

Case Study: “Killer Algae!”

The alga originated at the Oceanographic Museum of Monaco in 1984.

A cold-resistant strain of *Caulerpa* had been sent to them from a zoo in Germany, to use as a backdrop for tropical fish aquaria.

The museum released *Caulerpa* in the process of cleaning tanks, thinking it would die in the cold Mediterranean.

Case Study: “Killer Algae!”

Scientists and fisherman alike wanted to understand how this abundant and fast-spreading seaweed would affect marine habitats and fisheries.

How does one very abundant species influence the other species in the community?

Introduction

Although so far we have considered species interactions in two-way relationships, in reality, species experience multiple interactions that shape the communities in which they live.

What Are Communities?

Concept 15.1: Communities are groups of interacting species that occur together at the same place and time.

Interactions among multiple species give communities their character and function.

They make communities into something more than the sum of their parts.

What Are Communities?

In practical terms, defining a community requires using biological or physical guidelines.

A physically defined community might encompass all the species in a sand dune, a mountain stream, or a desert.

Figure 15.3 A Defining Communities

(A) Physically defined communities

What Are Communities?

A biologically defined community might include all the species associated with a kelp forest, a freshwater bog, or a coral reef.

A common species, such as kelp, wetland plants, or coral, is the basis for the community delineation.

Figure 15.3 B Defining Communities

(B) Biologically defined communities

What Are Communities?

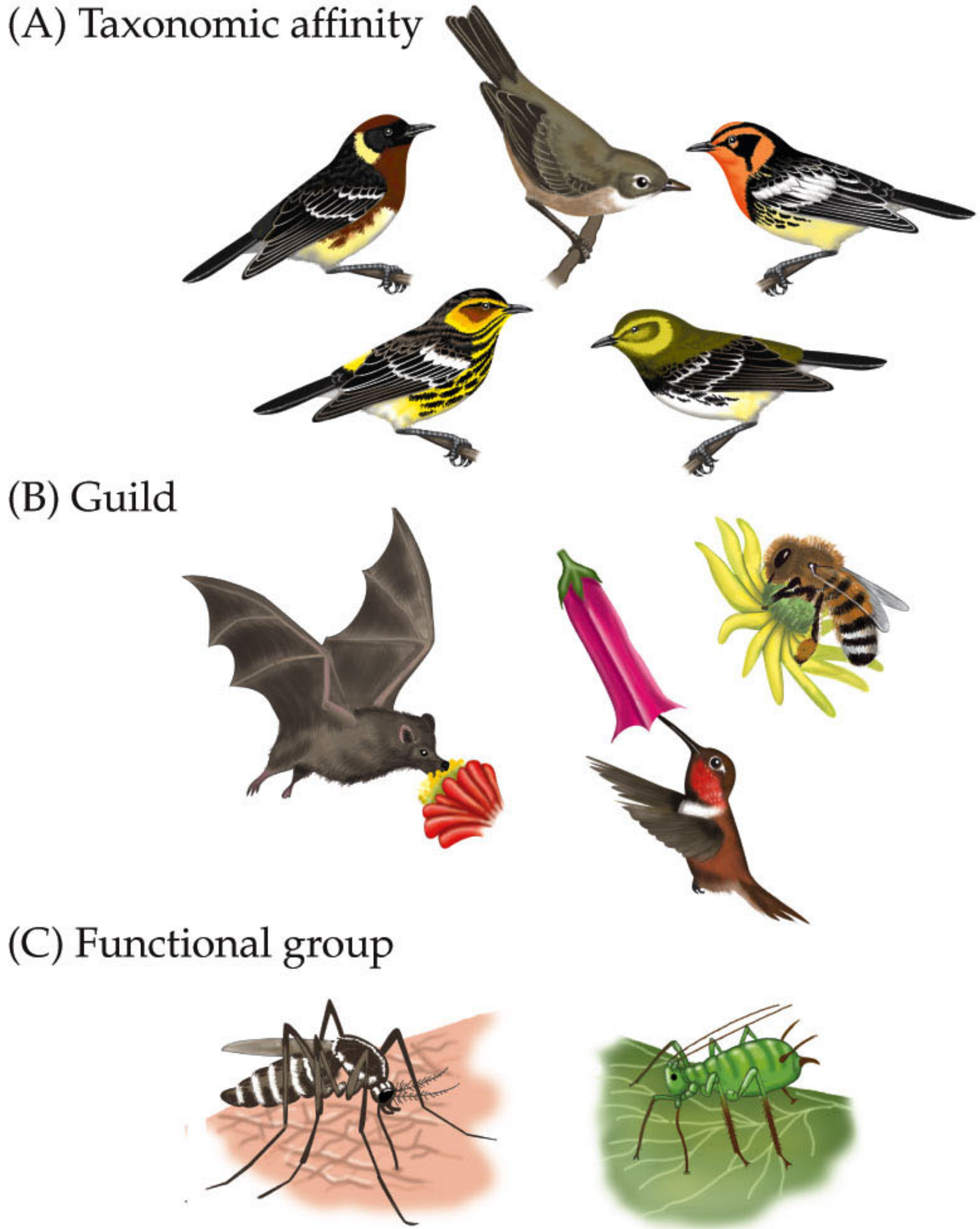
Counting all the species in a community is difficult to impossible, especially if small or relatively unknown species are considered.

Ecologists usually consider a subset of species when they define and study communities.

Subsets can be defined in several ways:

- Taxonomic affinity—a study might be confined to all bird species in a community.
- **Guilds**—groups of species that use the same resources.
- **Functional group**—species that function in similar ways, but do not necessarily use the same resources.

Figure 15.4 Subsets of Species in Communities



What Are Communities?

Food webs allow ecologists to organize species based on their trophic or energetic interactions.

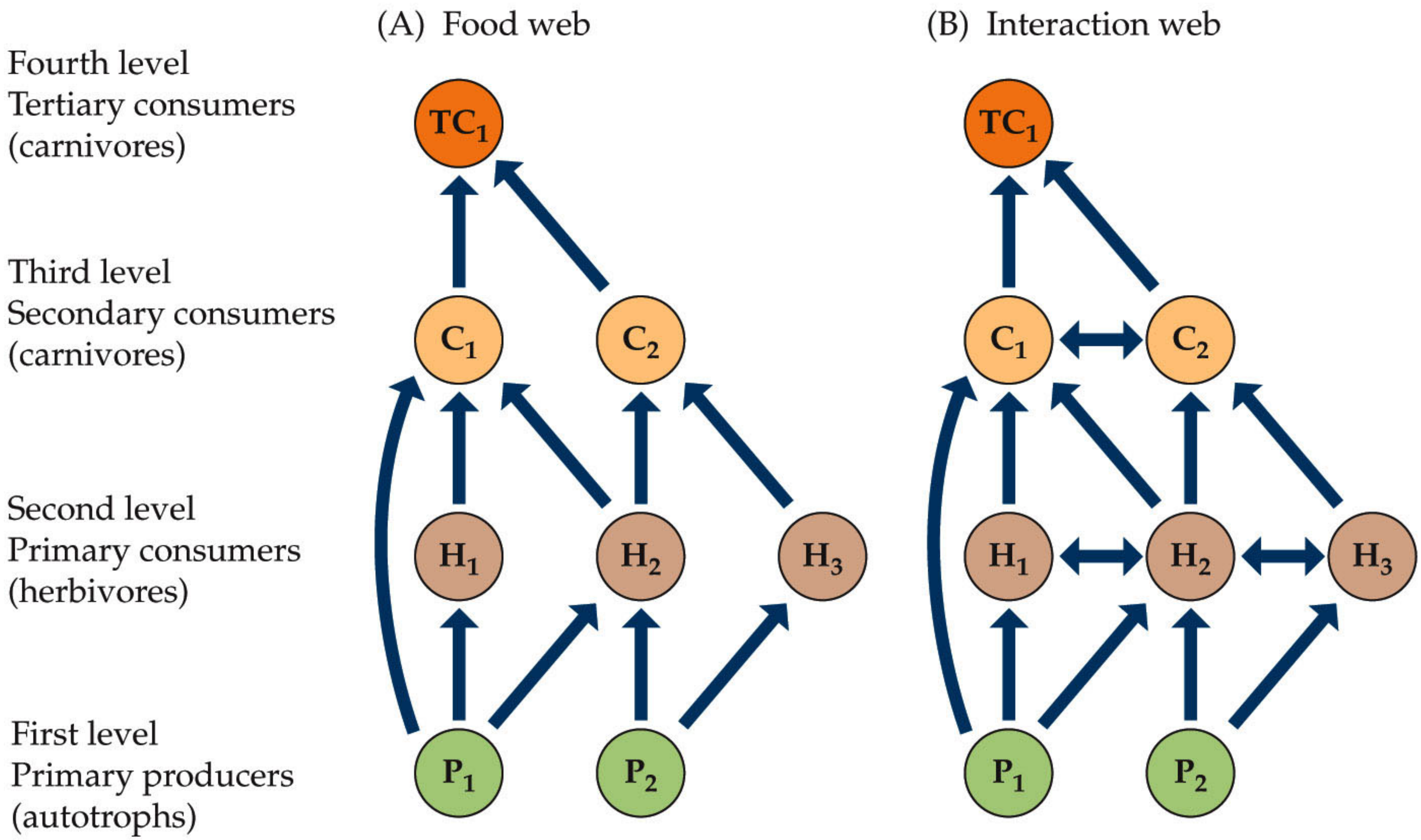
Trophic levels are groups of species that have similar ways of obtaining energy (e.g., primary producers, primary consumers).

Food webs tell little about the strength of interactions or their importance in the community.

Some species span two trophic levels, and some species change feeding status as they mature.

Some species are **omnivores**, feeding on more than one trophic level.

Figure 15.5 Four-Level Food and Interaction Webs



***ECOLOGY,* Figure 15.5**

Food webs also do not include nontrophic interactions (**horizontal interactions**, such as competition) which we know can influence community character.

Interaction webs more accurately describe both the trophic (vertical) and non-trophic (horizontal) interactions in a traditional food web.

Concept 15.2: Species diversity and species composition are important descriptors of community structure.

Communities vary significantly in the number of species they contain.

Community structure is the set of characteristics that shape communities.

Species richness—the number of species in a community.

Species evenness—relative abundances compared with one another.

Species diversity combines species richness and species evenness.

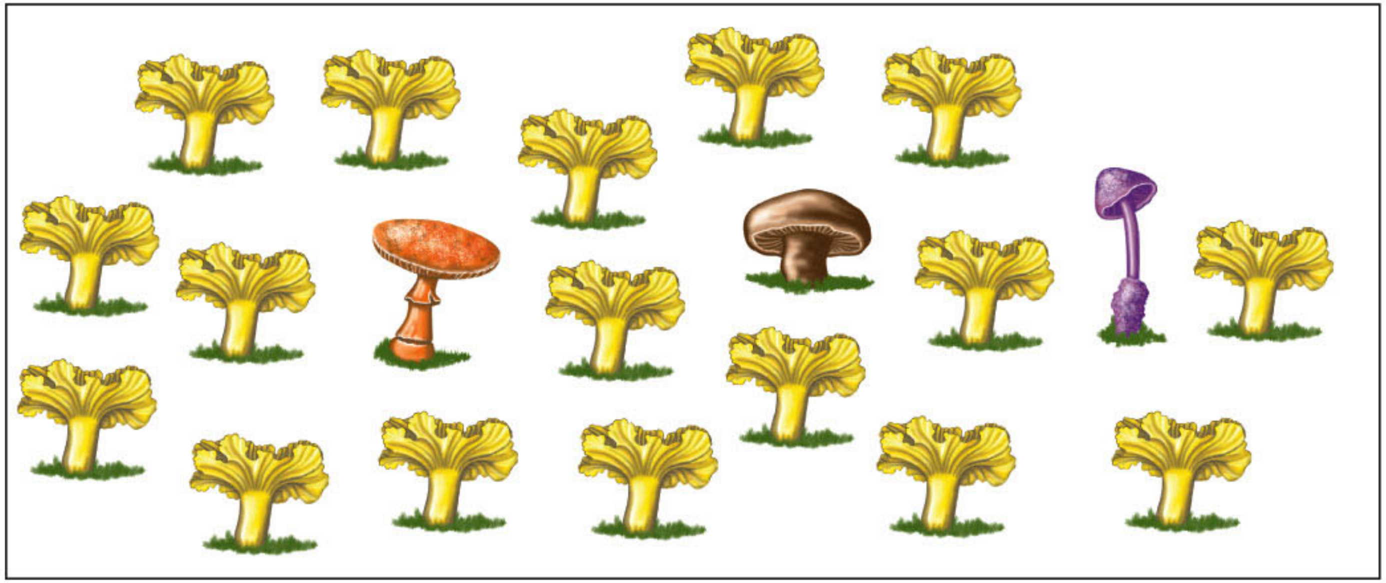
Example: Two communities with four species each (species richness equal).

In community A, one species constitutes 85% of the individuals, the other species 5% each.

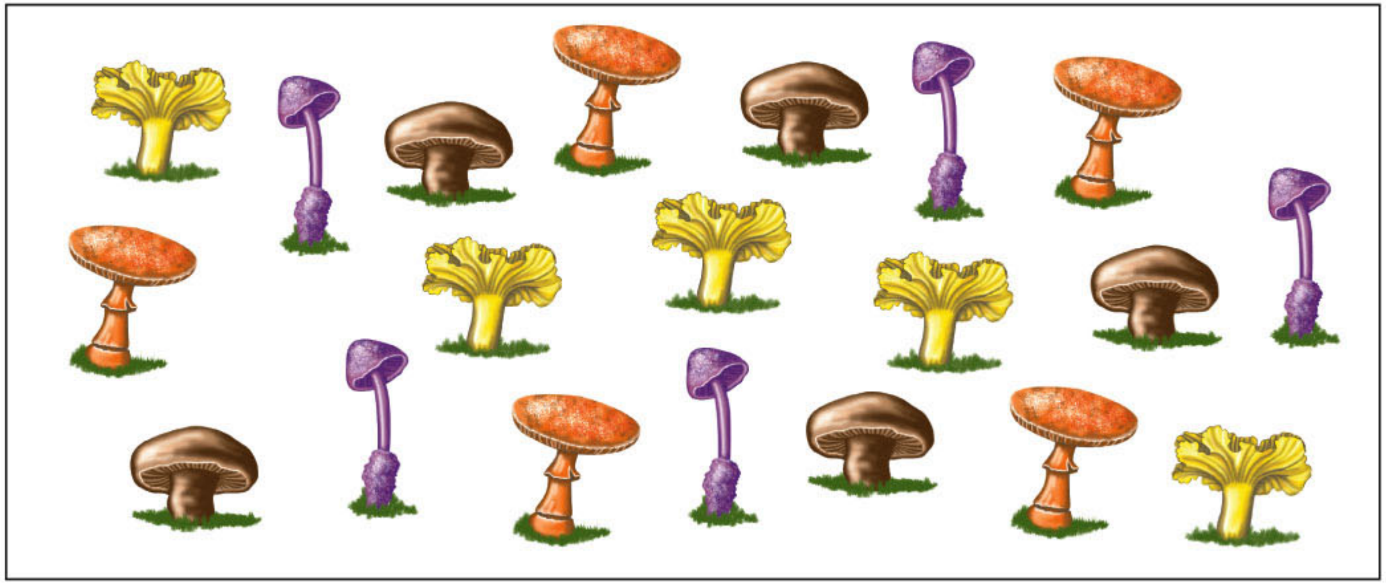
In community B, the abundance is equally divided, each species is 25%. This community has higher diversity.

Figure 15.6 Species Richness and Species Evenness

Community A



Community B



ECOLOGY, Figure 15.6

There are several quantitative species diversity indices. The one most commonly used is the **Shannon index**:

$$H = -\sum_{i=1}^{s} p_i \ln(p_i)$$

p_i = proportion of individuals in the *i*th species

s = number of species in the community

TABLE 15.1

Calculation of the Shannon Index for Communities A and B in Figure 15.6

COMMUNITY A

Species	Abundance	Proportion (p_i)	ln (p_i)	p_i ln (p_i)
Yellow	17	0.85	–0.163	–0.139
Orange	1	0.05	–2.996	–0.150
Purple	1	0.05	–2.996	–0.150
Brown	1	0.05	–2.996	–0.150
Total	20	1.00		–0.586

$$H = -\sum_{i=1}^{S} p_i \ln(p_i) = 0.586$$

TABLE 15.1

Calculation of the Shannon Index for Communities A and B in Figure 15.6

COMMUNITY B

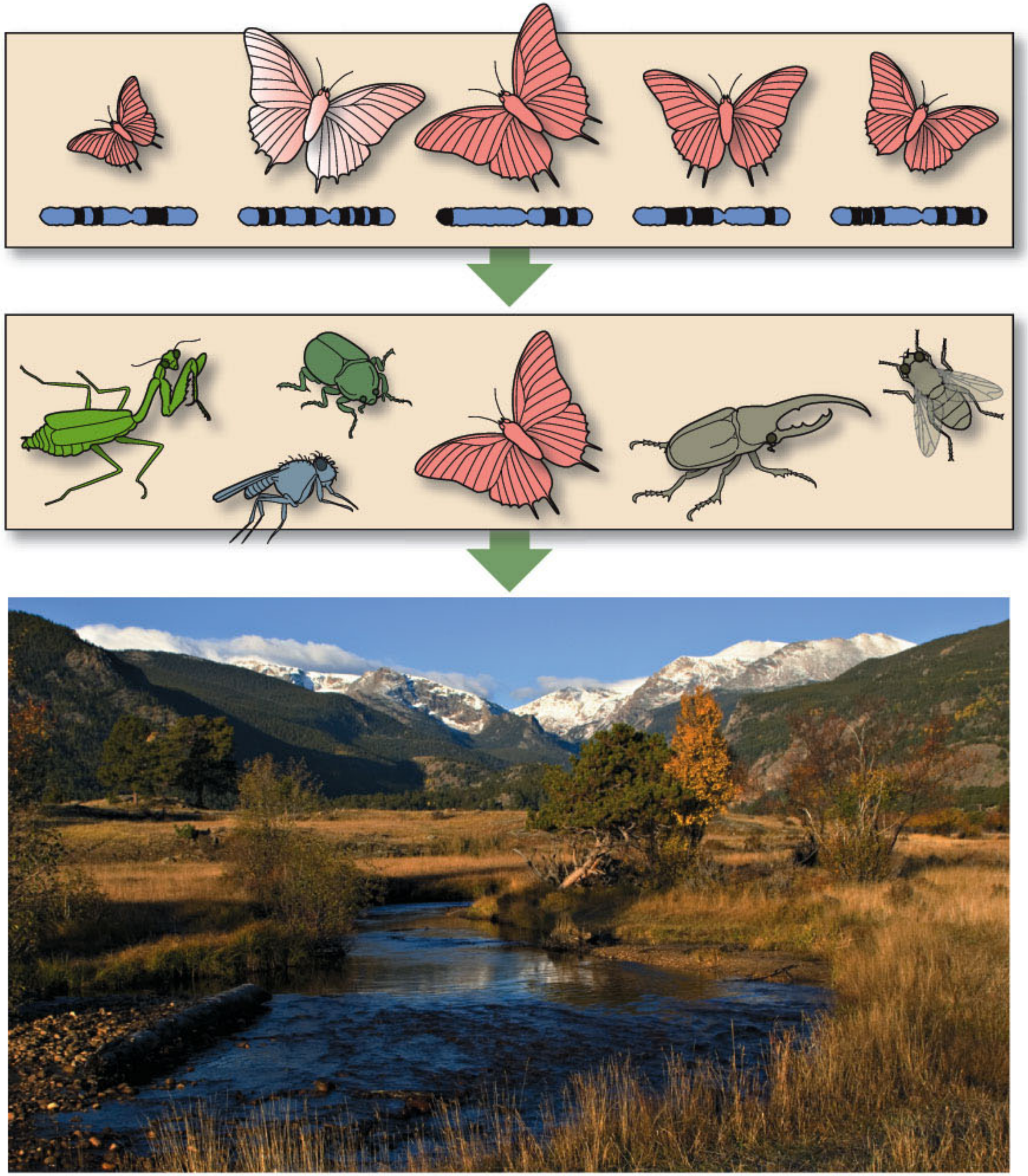
Species	Abundance	Proportion (p_i)	ln (p_i)	p_i ln (p_i)
Yellow	5	0.25	–1.386	–0.347
Orange	5	0.25	–1.386	–0.347
Purple	5	0.25	–1.386	–0.347
Brown	5	0.25	–1.386	–0.347
Total	20	1.00		–1.388

$$H = -\sum_{i=1}^{S} p_i \ln\left(p_i\right) = 1.388$$

Species diversity (and biodiversity) is often used more broadly to mean the number of species in a community.

Biodiversity describes the diversity of important ecological entities that span multiple spatial scales, from genes to species to communities. Implicit is the interconnectedness of all components of diversity.

Figure 15.7 Biodiversity Considers Multiple Spatial Scales



Community Structure

Genetic diversity affects the viability of populations; which in turn affects species diversity within a community.

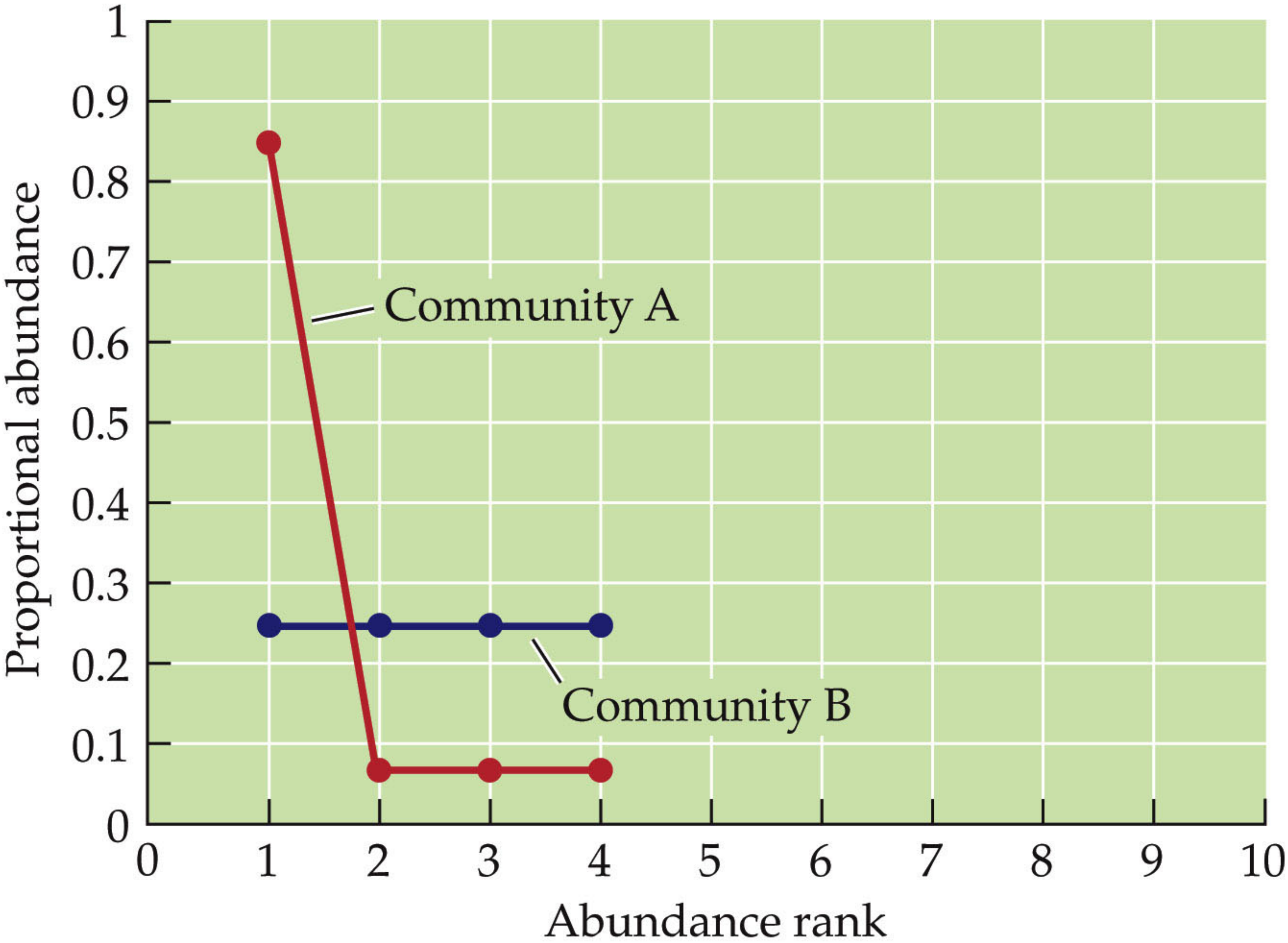
The number of different kinds of communities in an area is critical to diversity at larger regional and latitudinal scales.

Species diversity indices allow ecologists to compare different communities.

Graphical representations of species diversity can give a more explicit view of commonness or rarity.

Rank abundance curves plot the proportional abundance of each species (p_i) relative to the others in rank order.

Figure 15.8 Are Species Common or Rare?



ECOLOGY, Figure 15.8

Community Structure

Relative abundances can suggest the types of species interactions that might occur.

Example: In Community A, the dominant species might have a strong negative effect on the three rare species.

Experiments that add or remove species are used to explore these relationships.

Community Structure

Species diversity and rank abundance curves were determined for two soil bacteria communities in pastures in Scotland.

One pasture had been fertilized regularly.

Bacteria species can be identified quickly using DNA sequencing of 16S ribosomal DNA. The bacteria can then be grouped using phylogenetic analysis.

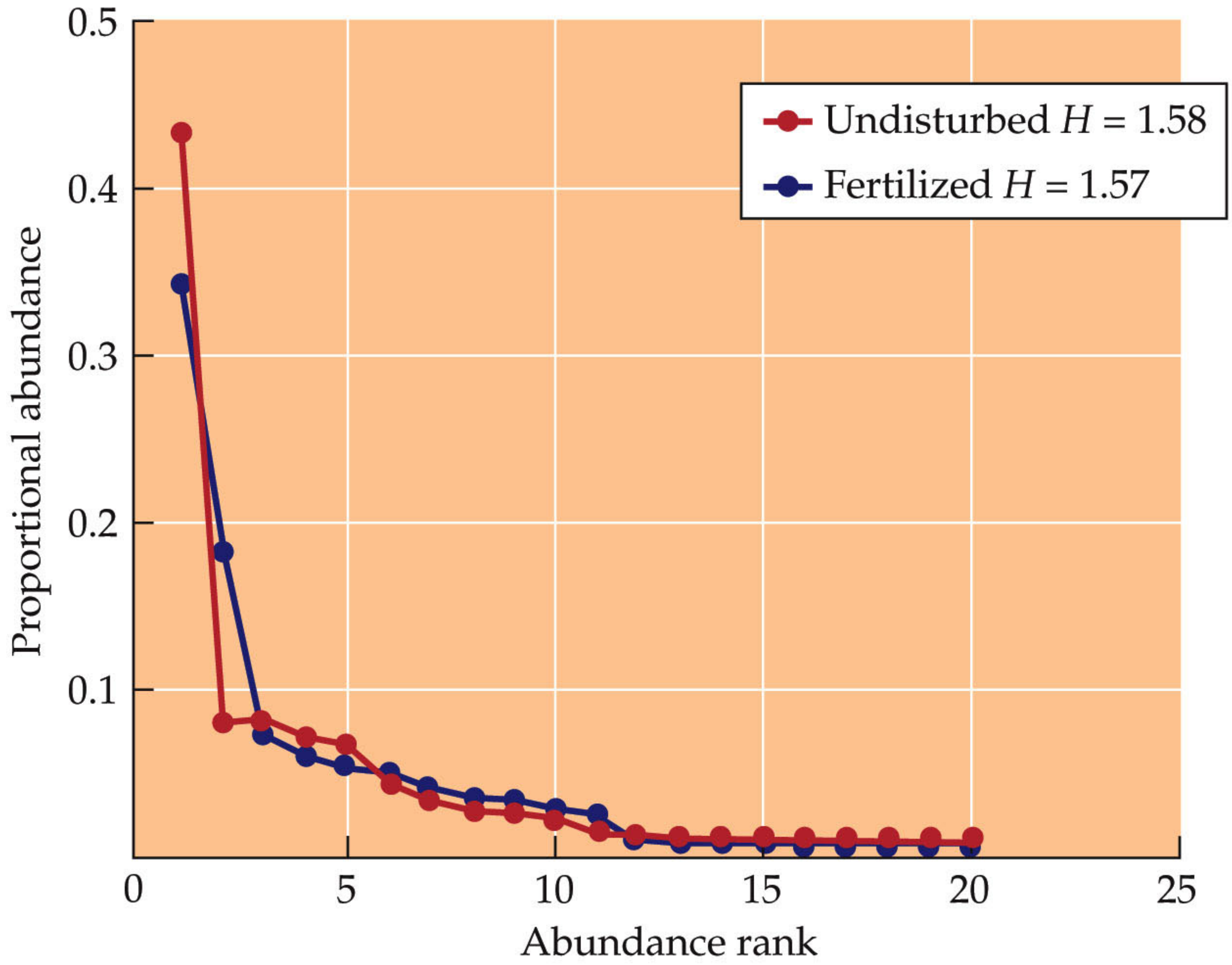
Community Structure

McCaig et al. (1999) found 22 phylogenetic groups of bacteria.

Both pastures had very similar community structure. A few species were abundant; most species were rare.

Whether this pattern tells us something about the species and their interactions is largely unknown, especially for microbial communities.

Figure 15.9 Bacterial Diversity in Pastures in Scotland

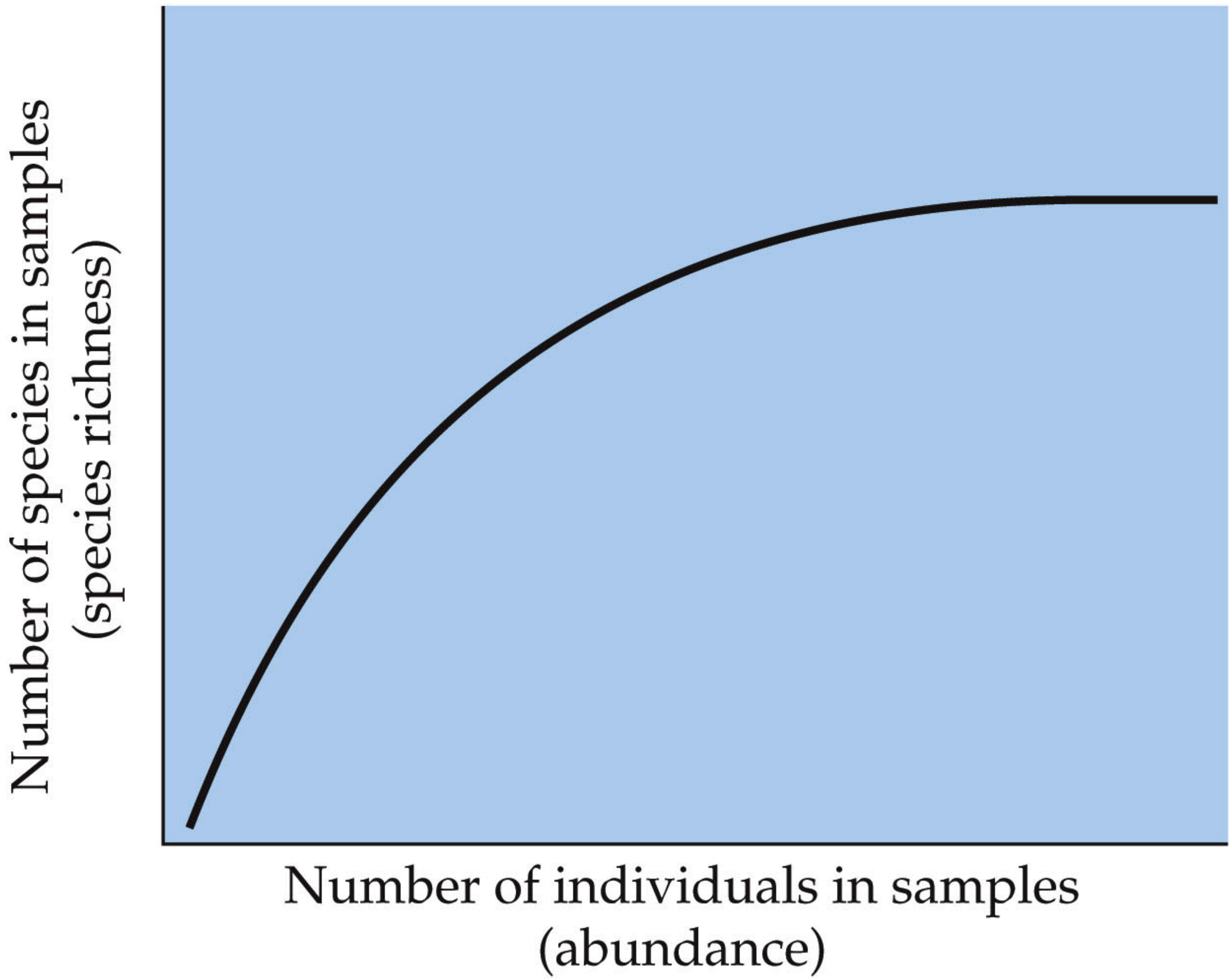


ECOLOGY, Figure 15.9

Species accumulation curves—species richness is plotted as a function of the total number of individuals that have been counted with each sample.

These curves can help determine when most or all of the species in a community have been observed.

Figure 15.10 When Are All the Species Sampled?



ECOLOGY, Figure 15.10

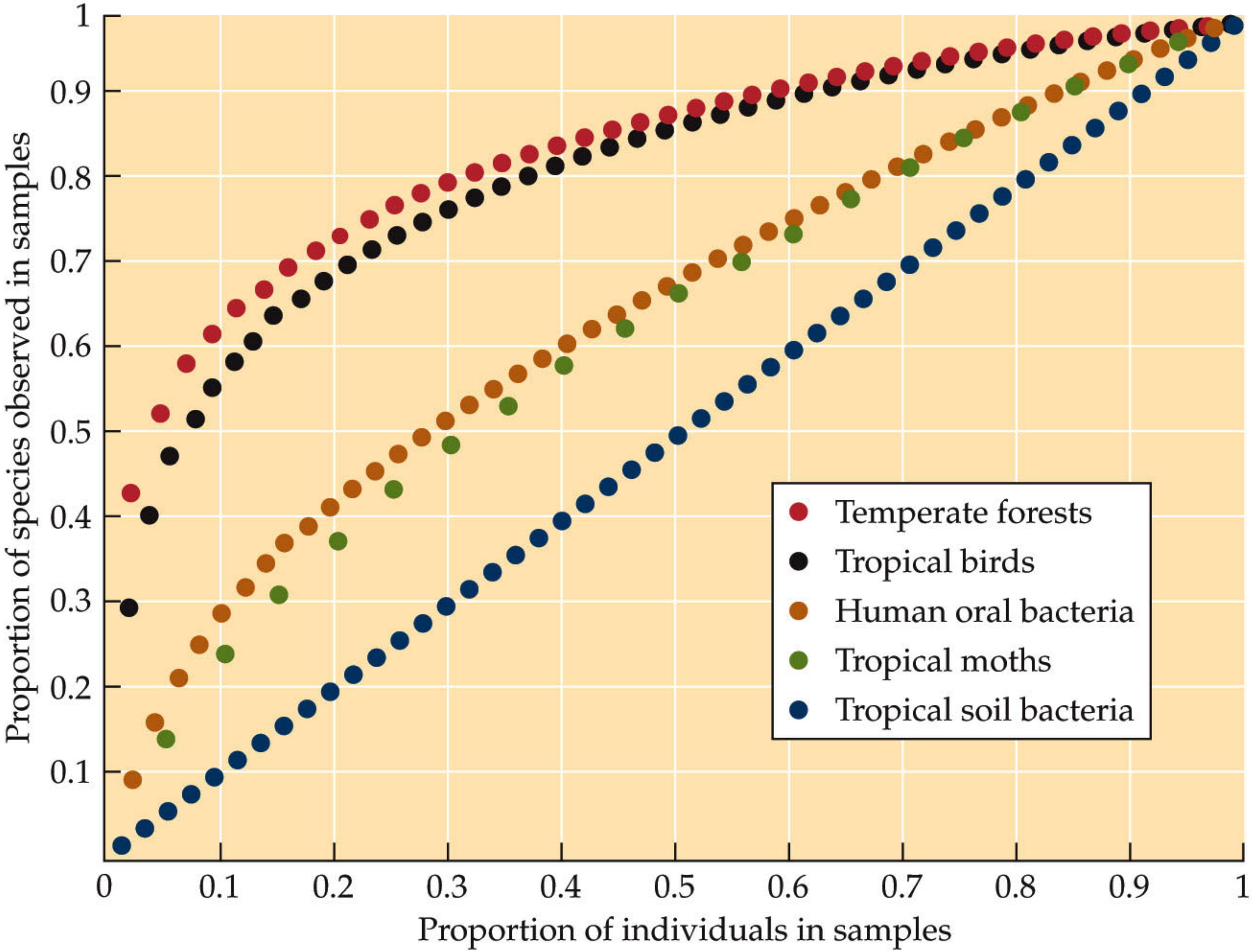
The more samples taken, the more individuals will be added, and the more species will be found.

At some point, the curve will reach a threshold at which no new species are added despite additional sampling.

Hughes et al. (2001) compared species accumulation curves for 5 different communities:

- Temperate forest in Michigan.
- Tropical bird community in Costa Rica.
- Tropical moth community in Costa Rica.
- Bacterial community from a human mouth.
- Bacterial community from tropical soils.

Figure 15.11 Communities Differ in Their Species Accumulation Curves



ECOLOGY, Figure 15.11

The 5 communities varied greatly in the amount of sampling effort necessary to determine their species richness.

The Michigan forest and Costa Rican bird community was adequately represented well before half the individuals were sampled.

But for tropical soil bacteria, more effort was needed to sample this extremely diverse community.

Spatial scale is also important.

For example, if we were to sample bacteria in tropical soils at the same scale as Costa Rican moths, the bacterial diversity would be immense in comparison.

The study also shows how little we know about community structure of rarely studied assemblages, such as microbial communities.

Species composition—the identity of species present in the community.

Two communities could have identical species diversity values, but have completely different species.

The identity of species is critical to understanding community structure.

Interactions of Multiple Species

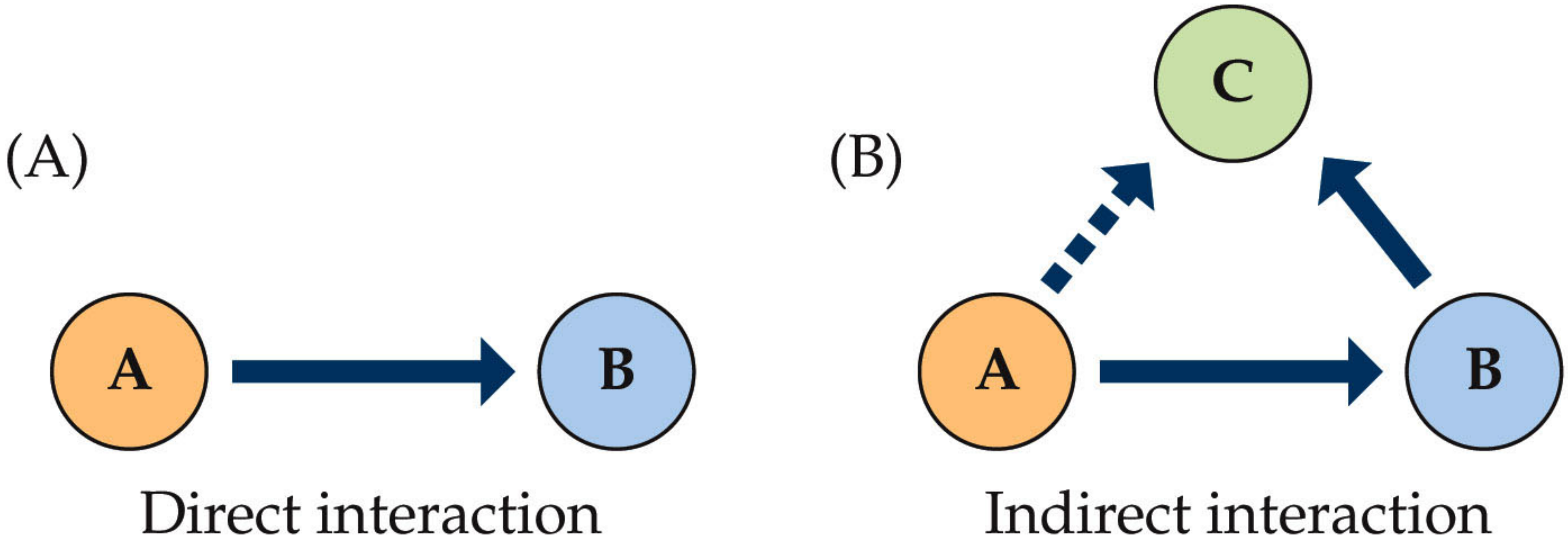
Concept 15.3: Communities can be characterized by complex networks of direct and indirect interactions that vary in strength and direction.

In a community, multiple species interactions generate a multitude of connections.

Direct interactions occur between two species (e.g., competition, predation, and facilitation).

Indirect interactions occur when the relationship between two species is mediated by a third (or more) species.

Figure 15.12 Direct and Indirect Species Interactions



Interactions of Multiple Species

Darwin first described the importance of indirect effects when he mused about the possible effect of cats on the flowers his district.

Pollination depends on bees; the bee population is influenced by mice that prey on bees' nests; mice are eaten by cats. A increase in the cat population could impact the flowers!

Interactions of Multiple Species

Indirect effects are often discovered by accident when species are experimentally removed to study the strength of direct interactions.

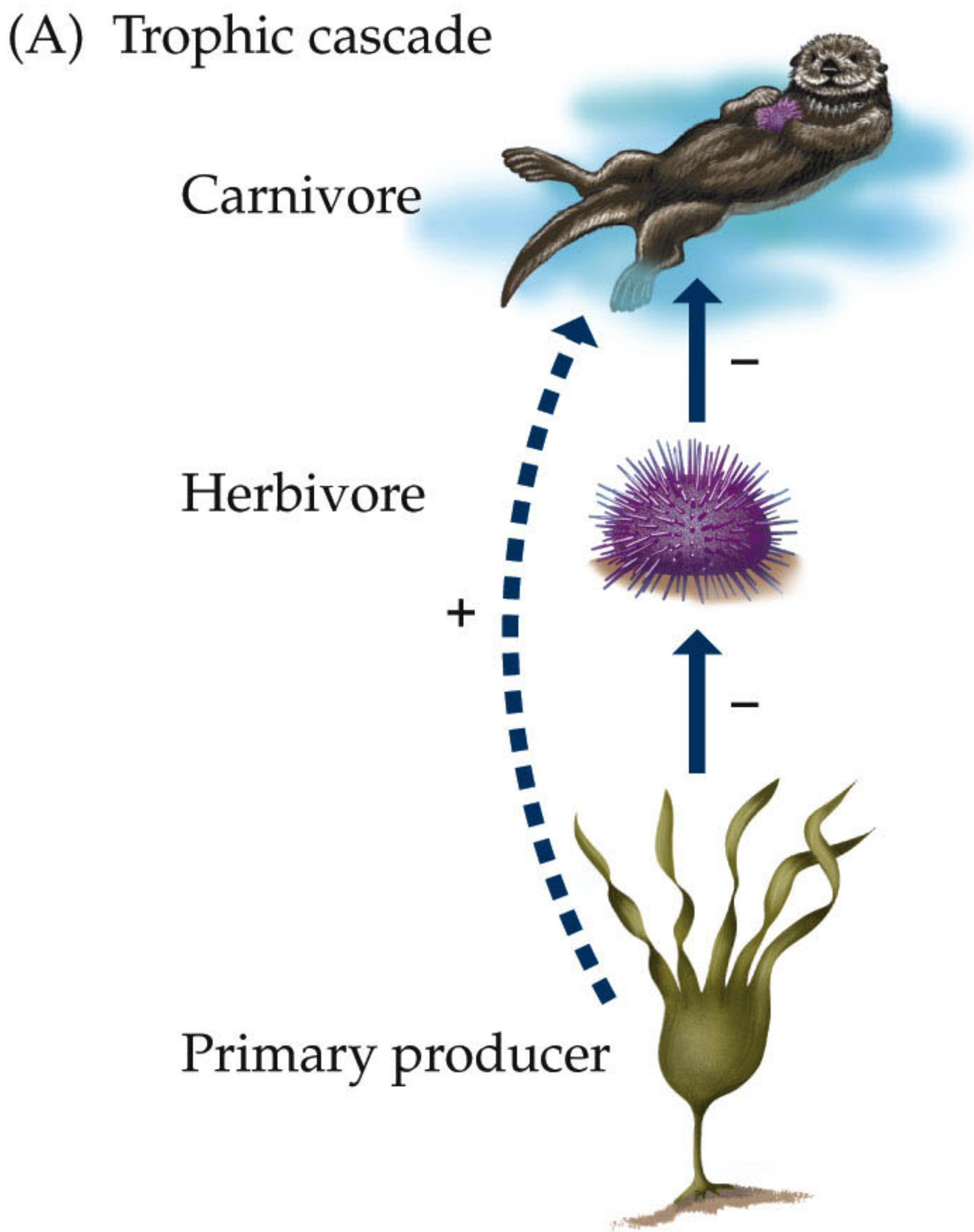
Example: An interaction web called a **trophic cascade**—a carnivore eats an herbivore (a direct negative effect on the herbivore). The decrease in herbivore abundance has a positive effect on a primary producer.

Interactions of Multiple Species

A tropic cascade example: The indirect regulation of kelp forests by the sea otter through its direct interaction with sea urchins along the west coast of North America.

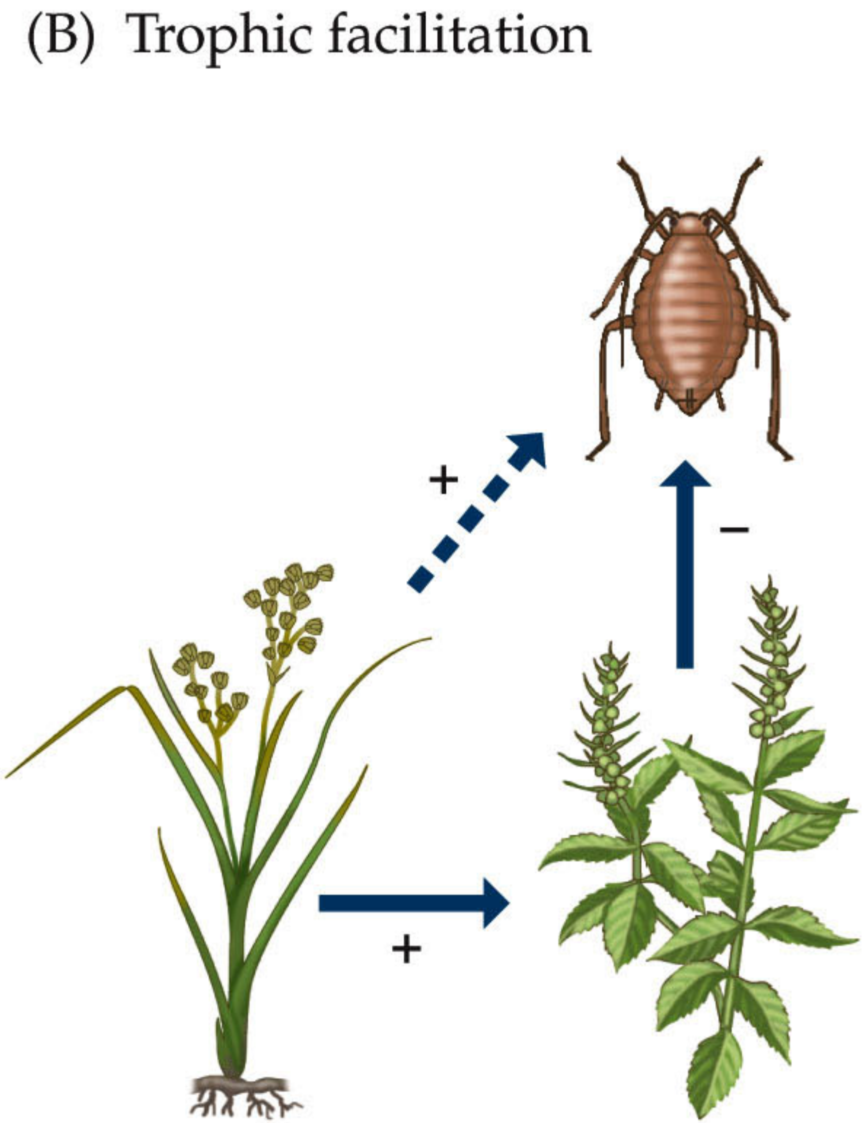
Kelp, in turn, can positively affect abundances of other seaweeds, which serve as habitat and food for marine invertebrates and fishes.

Figure 15.13 A Indirect Effects in Interaction Webs



Trophic facilitation occurs when a consumer is indirectly facilitated by a positive interaction between its prey and another species.

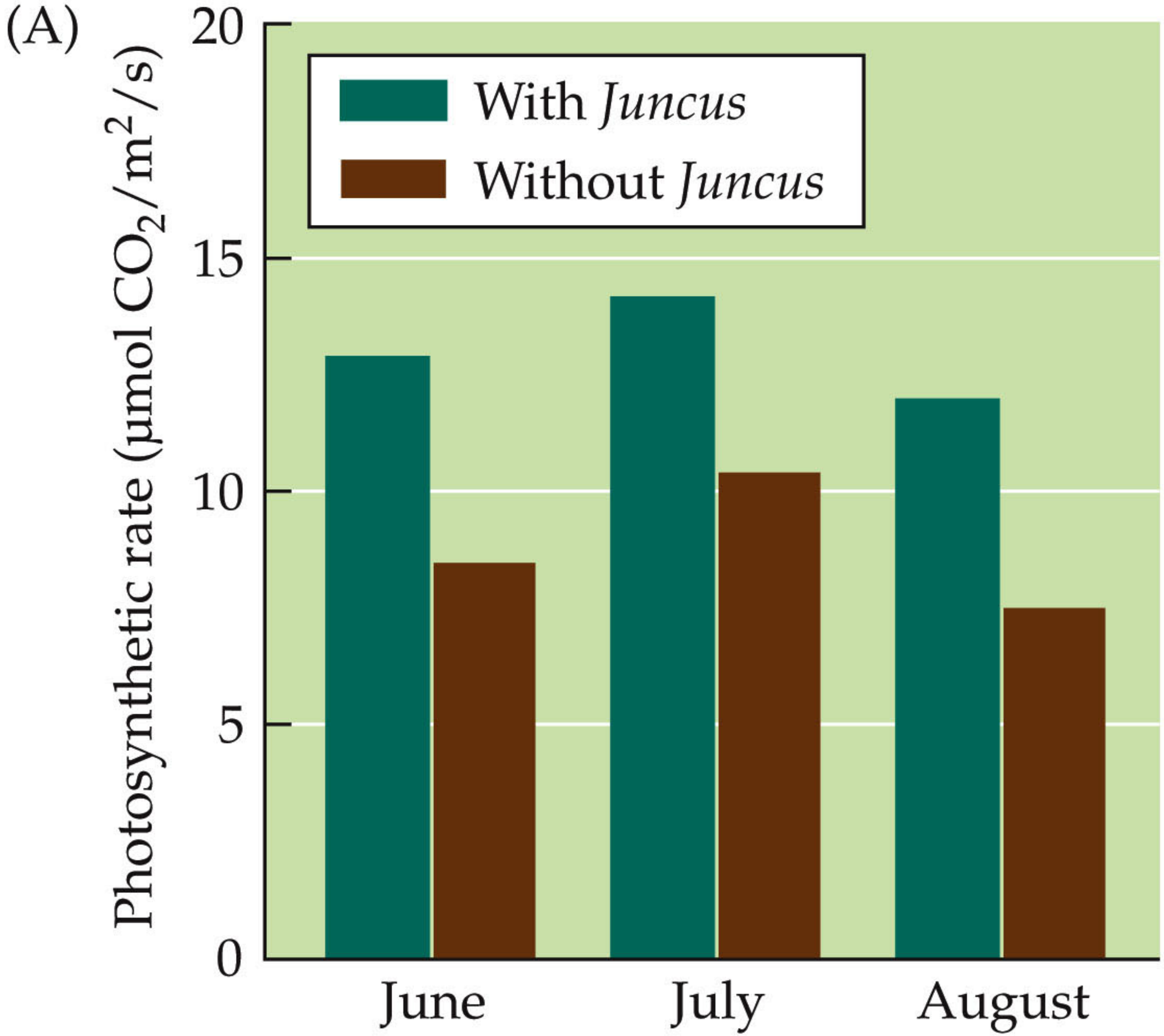
Figure 15.13 B Indirect Effects in Interaction Webs



In New England salt marshes, two plants—a sedge (*Juncus gerardii)*, and a shrub (*Iva frutescens)*—have a commensalistic relationship.

When *Juncus* is removed, *Iva* growth rate decreases, but removing *Iva* had no effect on *Juncus*.

Figure 15.14 A Results of Trophic Facilitation in a New England Salt Marsh



ECOLOGY, Figure 15.14 (Part 1)

Interactions of Multiple Species

When *Juncus* was removed, soil salinity increased and oxygen decreased. *Juncus* shades the soil surface, decreasing evaporation and salt buildup.

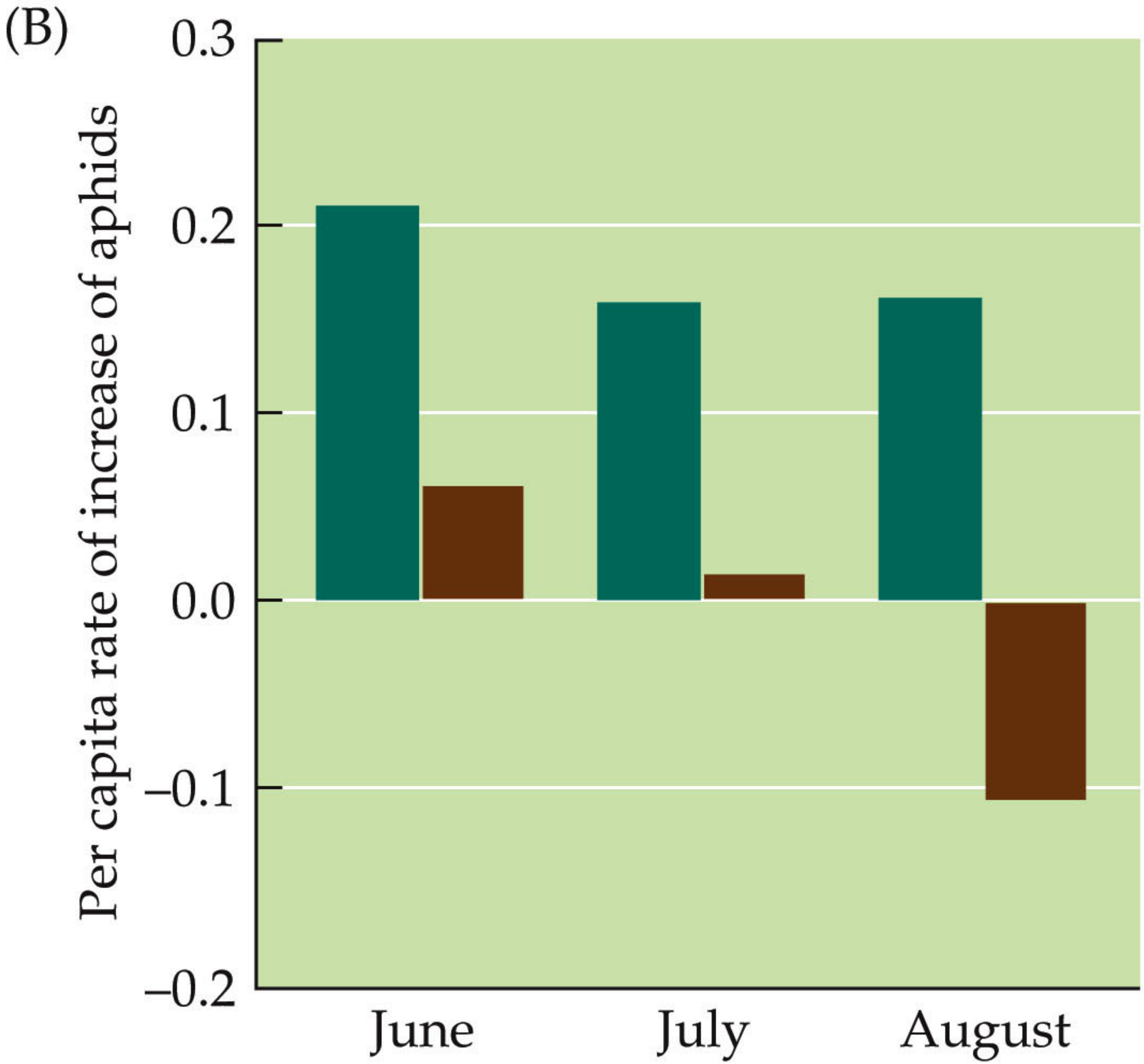
Juncus also has aerenchyma, tissue that allows oxygen to move to the roots, and some oxygen also moves into the soil where other plants can use it.

Interactions of Multiple Species

Hacker and Bertness (1996) also measured growth rates of aphids on *Iva*, with and without *Juncus*.

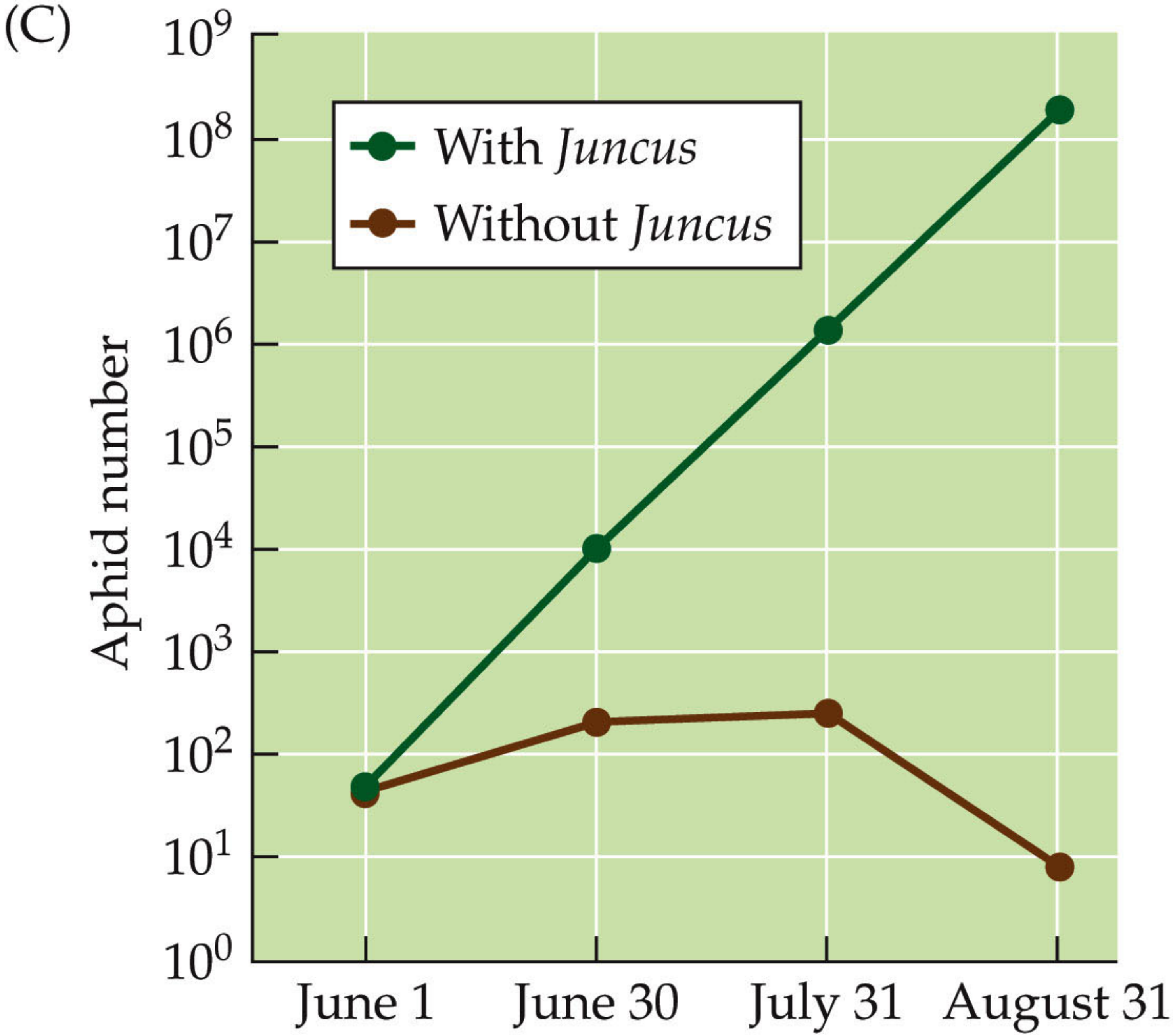
Aphids had more difficulty finding *Iva* in the presence of *Juncus*, but when they did, population growth rates were significantly higher.

Figure 15.14 B Results of Trophic Facilitation in a New England Salt Marsh



ECOLOGY, Figure 15.14 (Part 2)

Figure 15.14 C Results of Trophic Facilitation in a New England Salt Marsh



ECOLOGY, Figure 15.14 (Part 3)

Interactions of Multiple Species

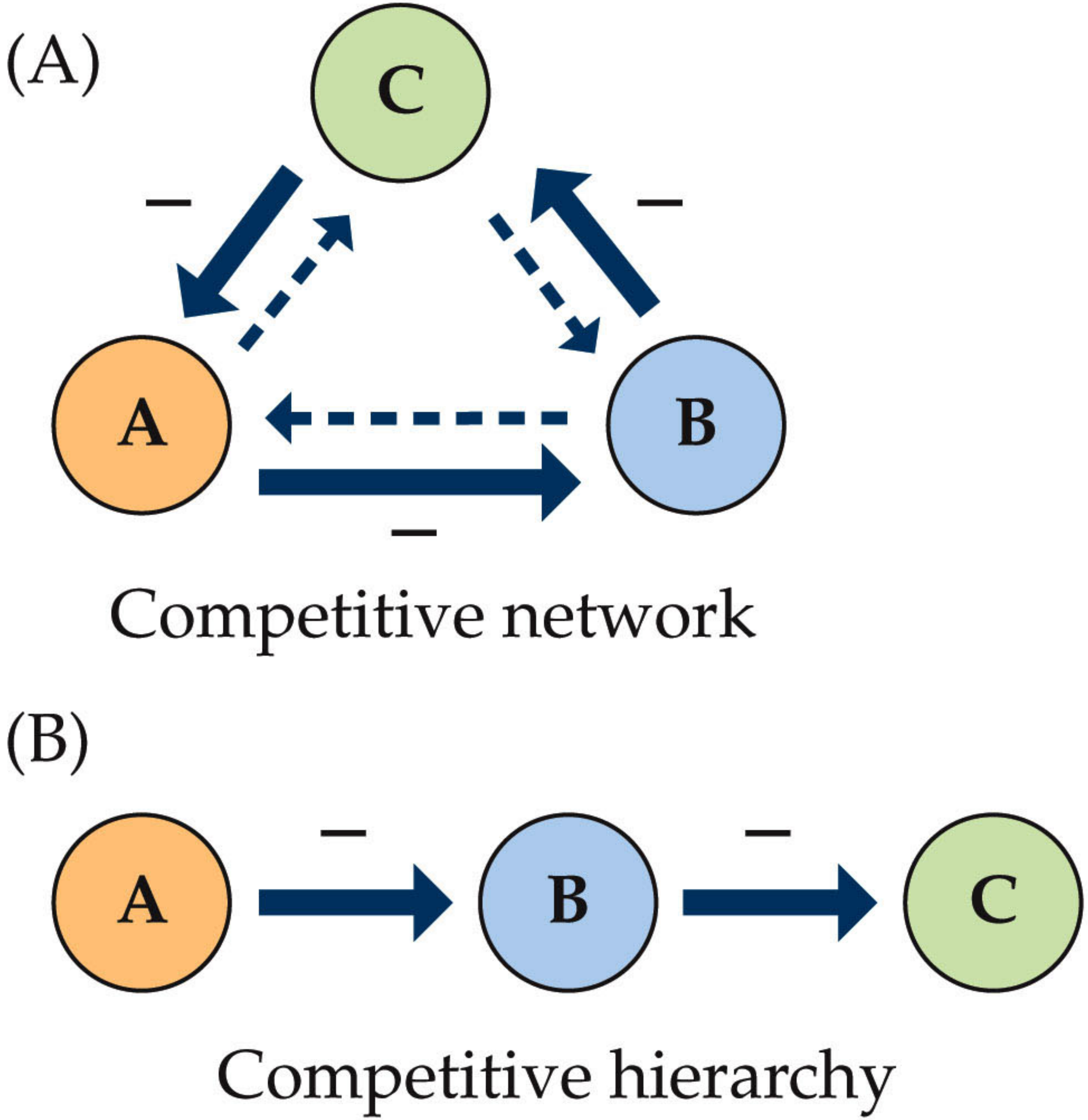
Interactions in trophic facilitation webs can have both positive (e.g., *Juncus* improves soil conditions for *Iva*) and negative effects (e.g., *Juncus* facilitates aphids that feed on *Iva*).

But it is the sum total of these effects that determine whether the interaction is beneficial or not.

Indirect effects can arise from multiple species interactions at one trophic level.

An hypothesis of Buss and Jackson (1979) to explain species richness and coexistence of competitors: Competitive interactions occur in a network fashion (i.e., every species negatively interacts with every other species).

Figure 15.15 Competitive Networks versus Competitive Hierarchies



Interactions of Multiple Species

Networks of interacting species may indirectly buffer strong direct competition, thus making competitive interactions weaker and more diffuse, and no one species dominates.

A hierarchical view of competition always results in one species dominating the interaction.

Interactions of Multiple Species

This was tested using invertebrates and algae on coral reefs.

These species compete for space by overgrowing one another.

The researchers looked at areas of overlap between species to determine proportion of wins (species on top) to losses (species on bottom).

Figure 15.16 Competitive Networks in Reef Organisms

ECOLOGY, Figure 15.16

Interactions of Multiple Species

No one species consistently won. The species interacted in a circular network rather than a linear hierarchy.

The results support the idea that competitive networks, by fostering diffuse and indirect interactions, can promote diversity in communities.

The strength of species interactions can be measured by removing one species (the *interactor species*) from the community and looking at the effect on the other species (the *target species*).

If removal of the interactor species results in a large decrease of the target species, the interaction is strongly positive. If the target species increases, the interaction is strongly negative.

Box 15.1 Measurements of Interaction Strength

Per capita interaction strength =

$$\frac{\ln\left(\frac{C}{E}\right)}{I}$$

C = # of target individuals with interactor present

E = # of target individuals with interactor absent

I = number of interactor individuals

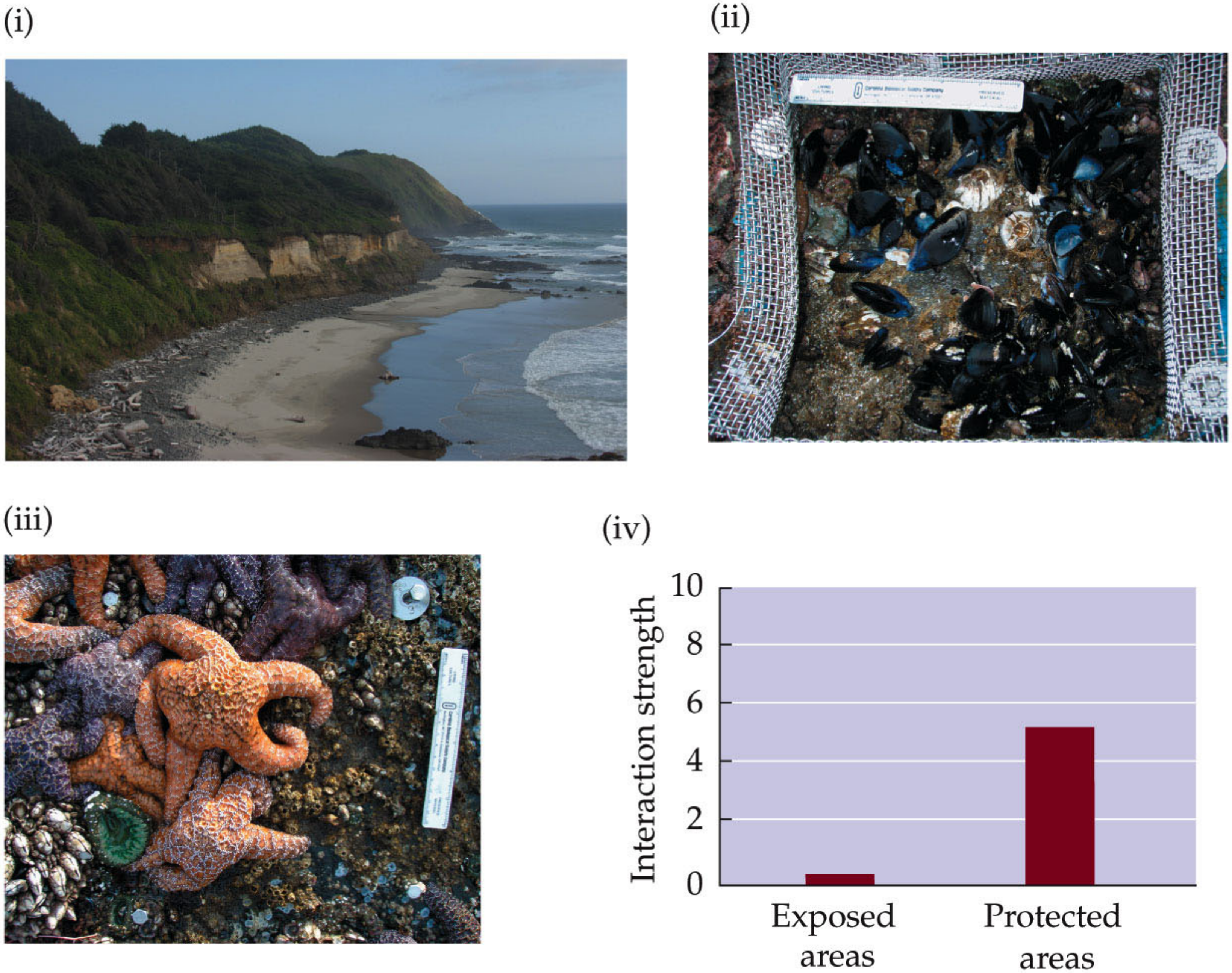
Box 15.1 Measurements of Interaction Strength

Interaction strength depends on the environmental context.

Menge et al. (1996) measured interaction strength of sea star (*Pisaster*) predation on mussels (*Mytilus*) in wave-exposed versus wave-protected areas.

Interaction strength was greater in wave-protected areas. *Pisaster* was a less efficient predator where waves were crashing in.

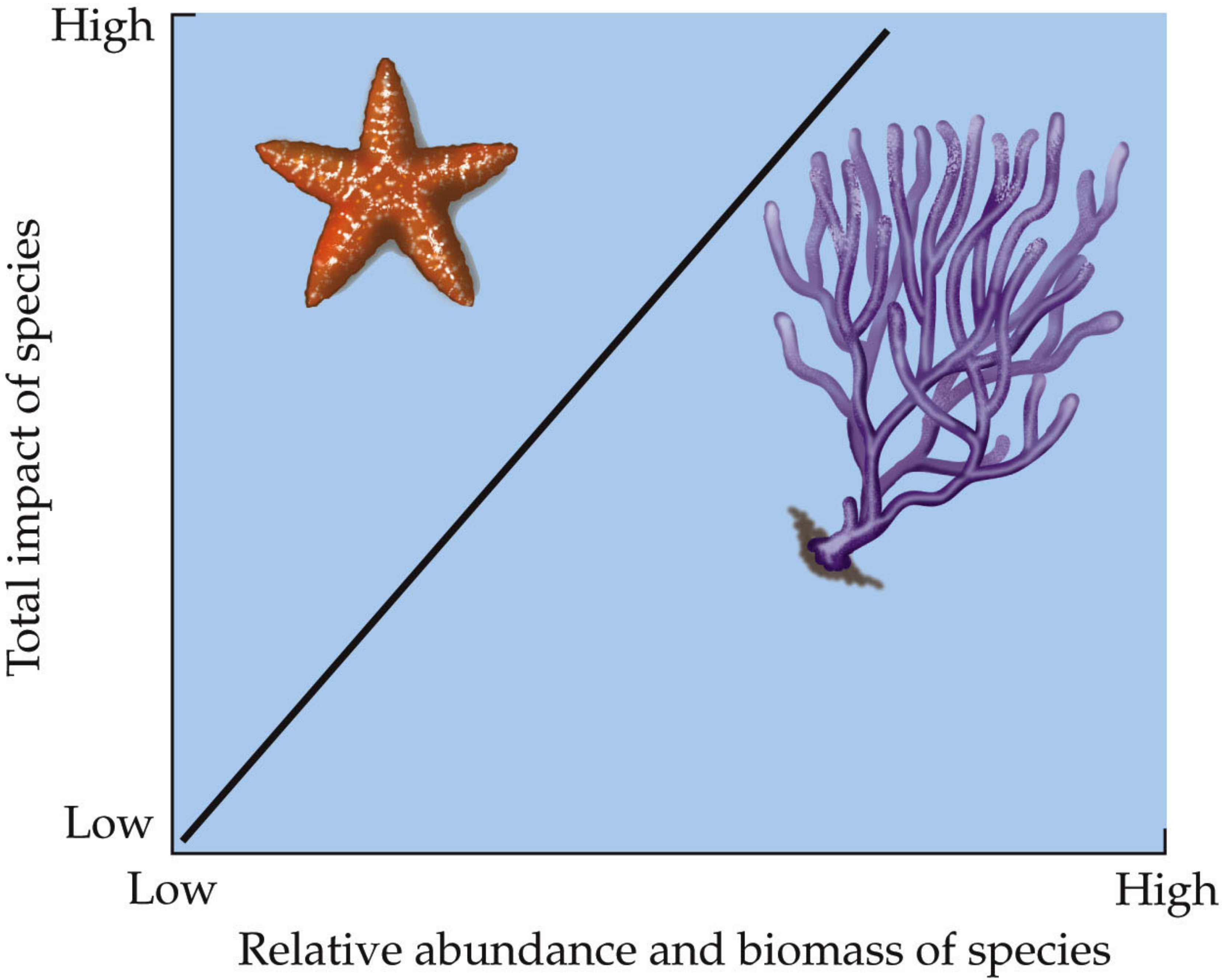
Box 15.1, Figure A How Much Does Predation by Sea Stars Matter? It Depends



Dominant species (**foundation species**) can have a large effect on other species and species diversity by virtue of high abundance or biomass.

Dominant species may also be dominant by virtue of being good competitors for space, nutrients, or light.

Figure 15.17 Dominant versus Keystone Species



ECOLOGY, Figure 15.17

Interactions of Multiple Species

Some dominant species are **ecosystem engineers**—they create, modify, or maintain physical habitat for themselves and other species.

Example: Trees—provide habitat and food; reduce light, wind and rainfall, which changes temperature and moisture conditions; roots increase weathering and soil aeration.

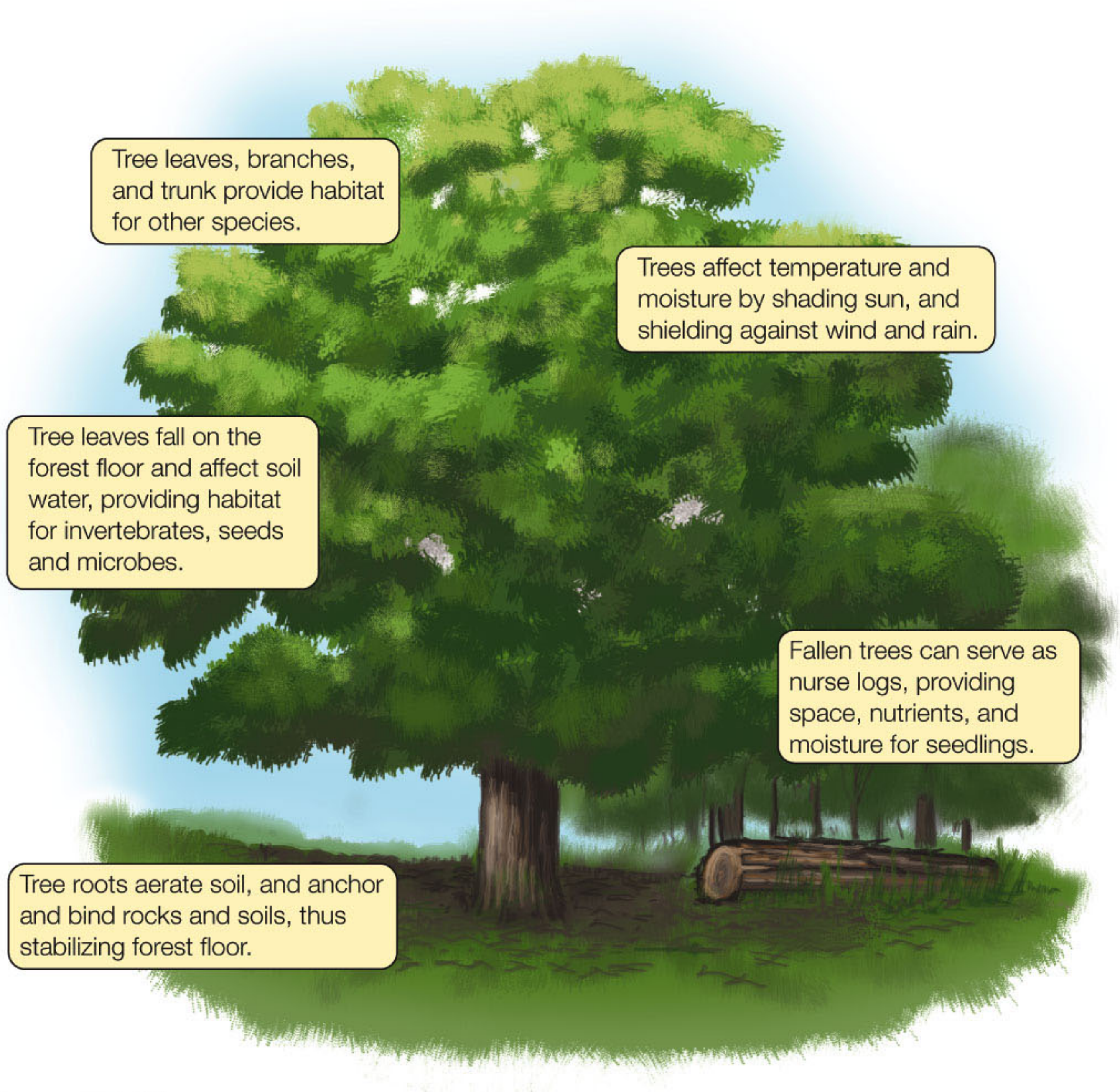
Interactions of Multiple Species

Leaf litter adds moisture and organic material to the forest floor, and habitat for many organisms.

A dead, fallen tree can be a “nurse log” providing space, nutrients, and moisture for tree seedlings.

Trees can have a large physical influence on the structure of the forest community.

Figure 15.18 Trees Are Dominant Species and Ecosystem Engineers



Keystone species have a strong effect because of their roles in the community.

Their effect is large in proportion to their biomass or abundance.

They usually influence community structure indirectly, via trophic means, as in the case of sea otters.

Interactions of Multiple Species

Some keystone species are ecosystem engineers.

Example: Beavers—a few individuals can have a large impact by building dams.

Dams can transform a swiftly flowing stream into a marsh with wetland plants.

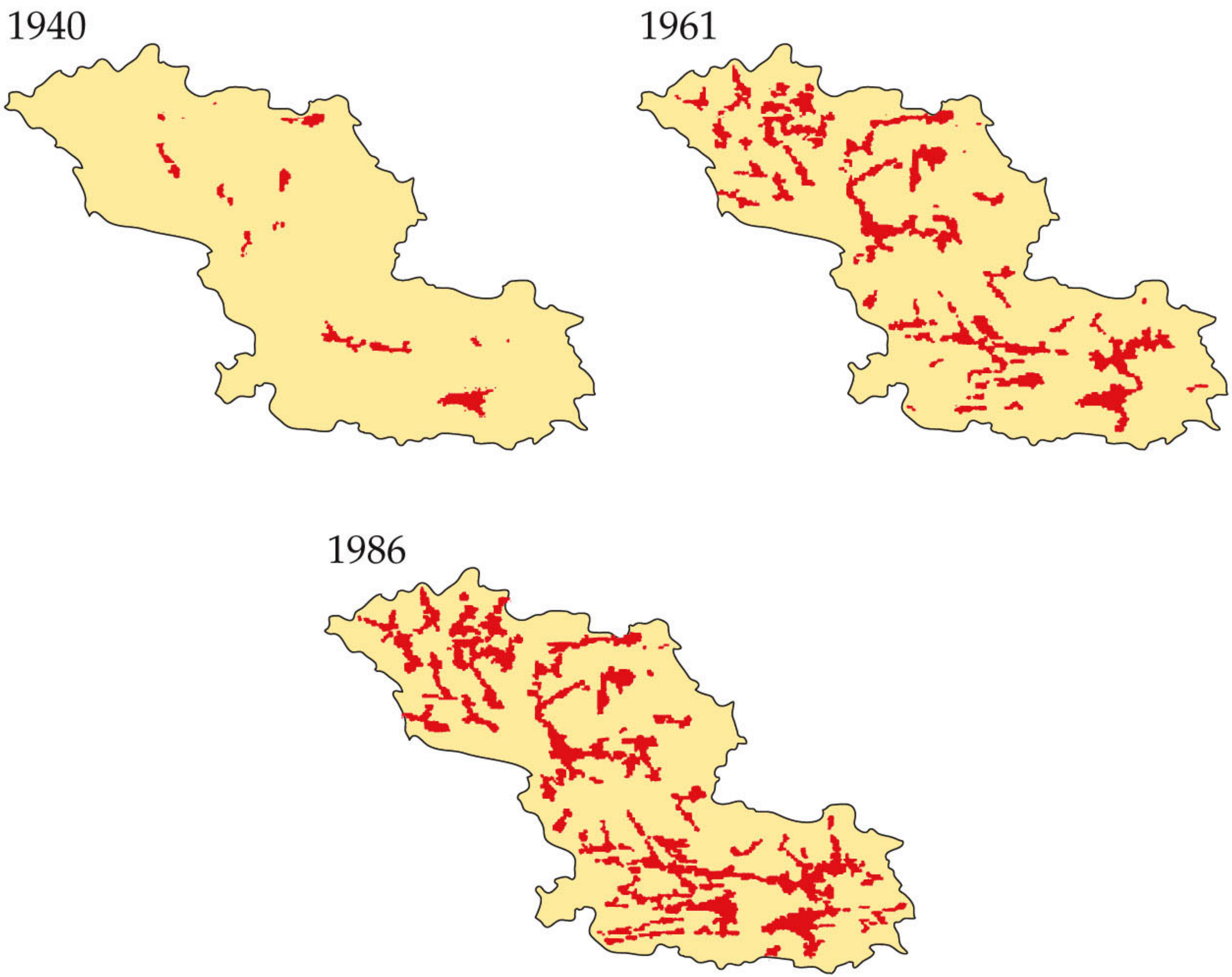
At the landscape level, beavers can create a mosaic of wetlands within a larger forest community, which increases regional biodiversity.

In one region of Minnesota where beavers were allowed to recolonize, there was a 13-fold increase in wetlands (Naiman et al.1988).

Figure 15.19 Beavers Are Keystone Species and Ecosystem Engineers (Part 1)

ECOLOGY, Figure 15.19 (Part 1)

Figure 15.19 Beavers Are Keystone Species and Ecosystem Engineers (Part 2)



ECOLOGY, Figure 15.19 (Part 2)

Interactions of Multiple Species

Context-dependent species interactions can change under different environmental conditions.

Some keystone species play important roles in their communities in one context, but not in another.

In northern California stream communities, the role of fish predators changes from year to year.

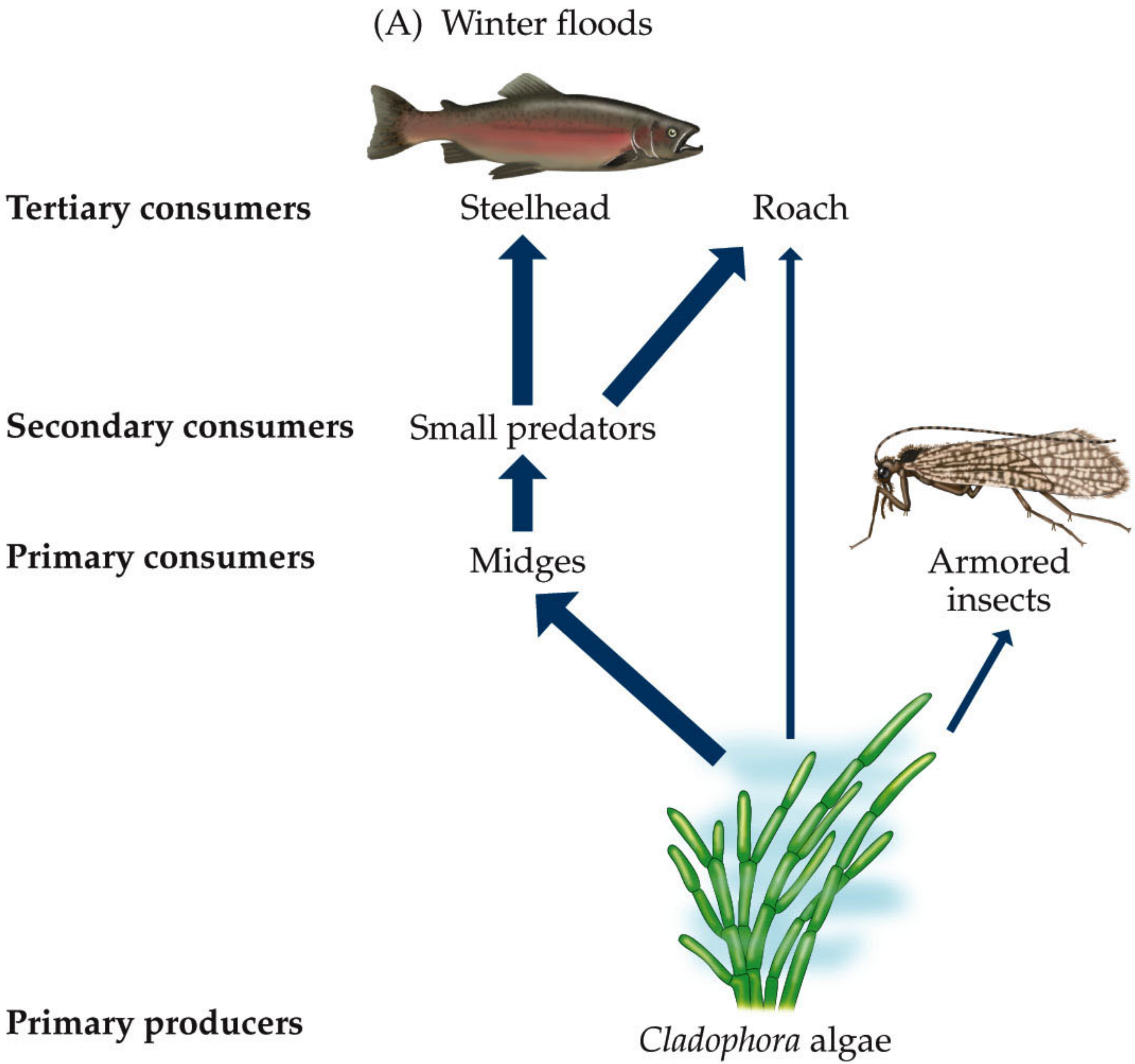
Winter floods scour most organisms from the stream bottom, especially armored herbivorous insects. This results in blooms of the green alga *Cladophora* in spring.

Interactions of Multiple Species

With few herbivores, *Cladophora* grows in large mats. Midges feed on the *Cladophora* and are in turn fed on by small predators.

The fish predators, steelhead and roach, decrease the size of the algal mats indirectly by eating the small predators which feed on midge larvae.

Figure 15.20 A Context Dependence in River Food Webs



Interactions of Multiple Species

In drought years, the rivers are controlled and no flooding and no scouring occurs.

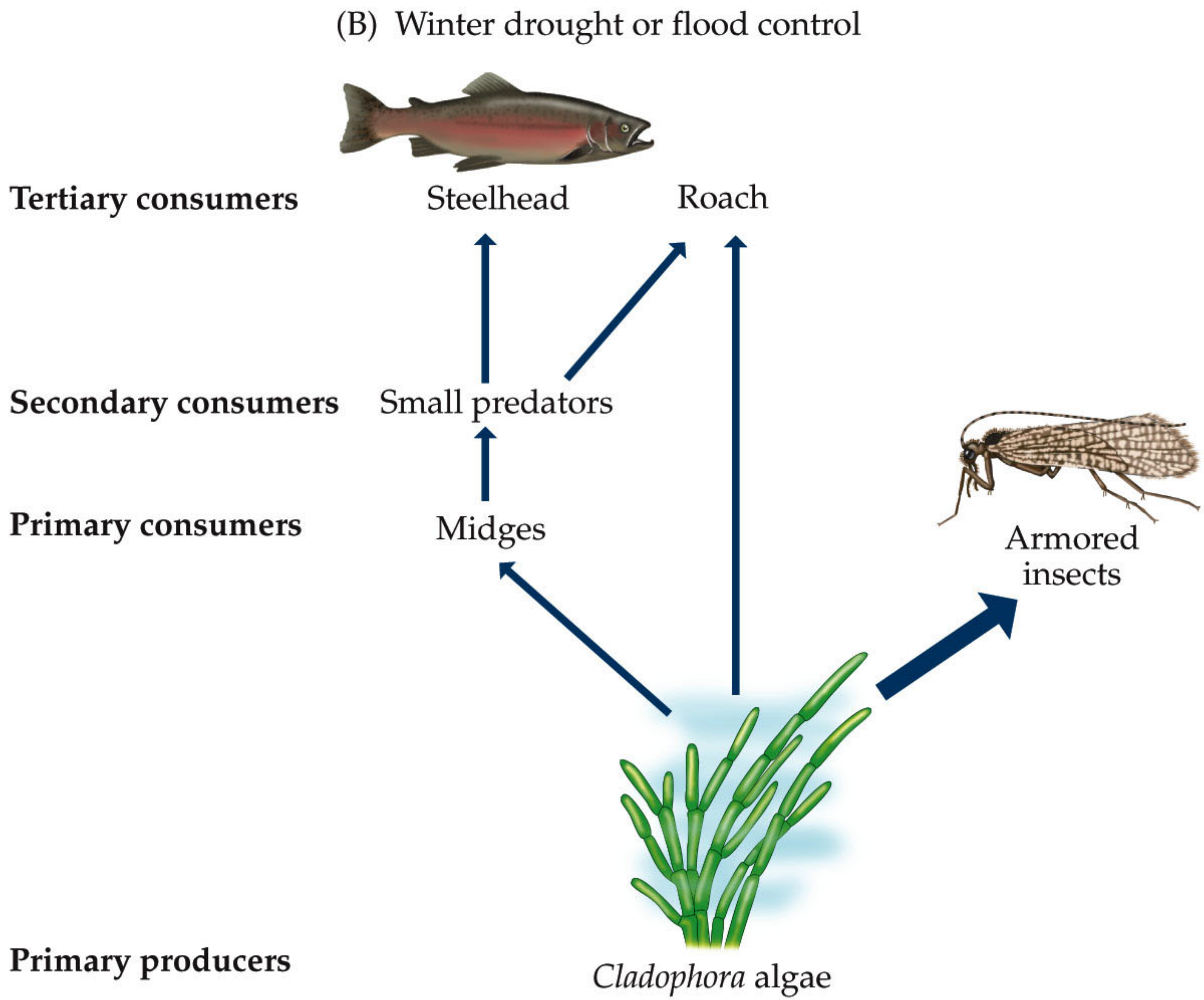
Cladophora does not form large mats because armored herbivorous insects are more abundant.

The armored insects are much less susceptible to predation than the midges and thus are not controlled by higher trophic levels.

Interactions of Multiple Species

The steelhead and roach, which were keystone species in other years, are now minor players in the food web.

Figure 15.20 B Context Dependence in River Food Webs



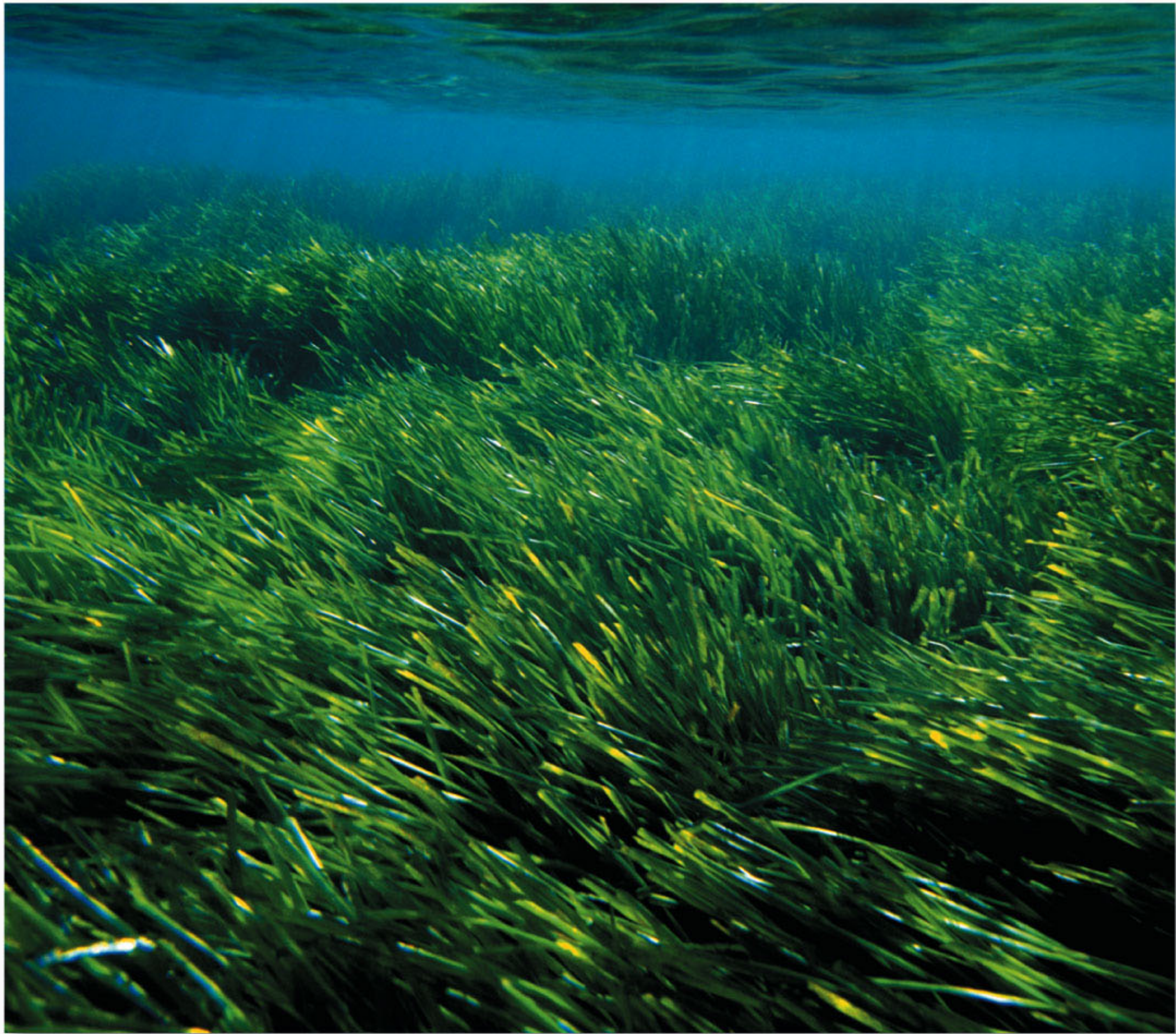
ECOLOGY, Figure 15.20 (Part 2)

Case Study Revisited: “Killer Algae!”

The introduction of *Caulerpa* to the Mediterranean dramatically changed the way native species interacted, and thus the structure and function of the native communities.

Seagrass meadows dominated by *Posidonia oceanica* were overgrown by *Caulerpa*. The seagrass meadows support a multitude of species.

Figure 15.21 A Mediterranean Seagrass Meadow



Case Study Revisited: “Killer Algae!”

Posidonia and *Caulerpa* have different growth cycles: *Posidonia* loses blades in the summer, when *Caulerpa* is most productive.

This allows *Caulerpa* to overtop *Posidonia* and dominate.

Case Study Revisited: “Killer Algae!”

Caulerpa acts as an ecosystem engineer, accumulating sediments around its roots more readily than *Posidonia*, which changes the invertebrate community.

There is also a significant drop in the numbers and sizes of fish after *Caulerpa* invades, suggesting the habitat is no longer suitable.

In 2000, *Caulerpa* was discovered near San Diego, California.

A team of scientists and managers from county, state, and federal agencies was immediately assembled to design an eradication plan.

It eventually took 6 years and $7 million to eradicate the alga.

Connections in Nature: Stopping Invasions Requires Commitment

This was a rare success story, made possible by the immediate actions of scientists, managers, and politicians.

Molecular evidence was used to determine the origin of the *Caulerpa*. Its DNA was identical to *Caulerpa* in the Mediterranean and public aquaria around the world. How the species was introduced is still unknown.

Connections in Nature: Stopping Invasions Requires Commitment

Subsequent invasions in Australia and Japan have been determined to be genetically identical to the original German strain.

Trade of this alga in aquarium circles poses a global threat to nearshore temperate marine environments.

Legislation is now in place to ban the “killer alga” from a number of other countries.