16

Change in Communities

- *Case Study:* A Natural Experiment of Mountainous Proportions
- Agents of Change
- Basics of Succession
- Mechanisms of Succession
- Alternative Stable States
- *Case Study Revisited*
- *Connections in Nature*: Primary Succession and Nitrogen-Fixing Bacteria

Case Study: A Natural Experiment of Mountainous Proportions

Figure 16.1 Once a Peaceful Mountain

Mt. St. Helens

May 18, 1980

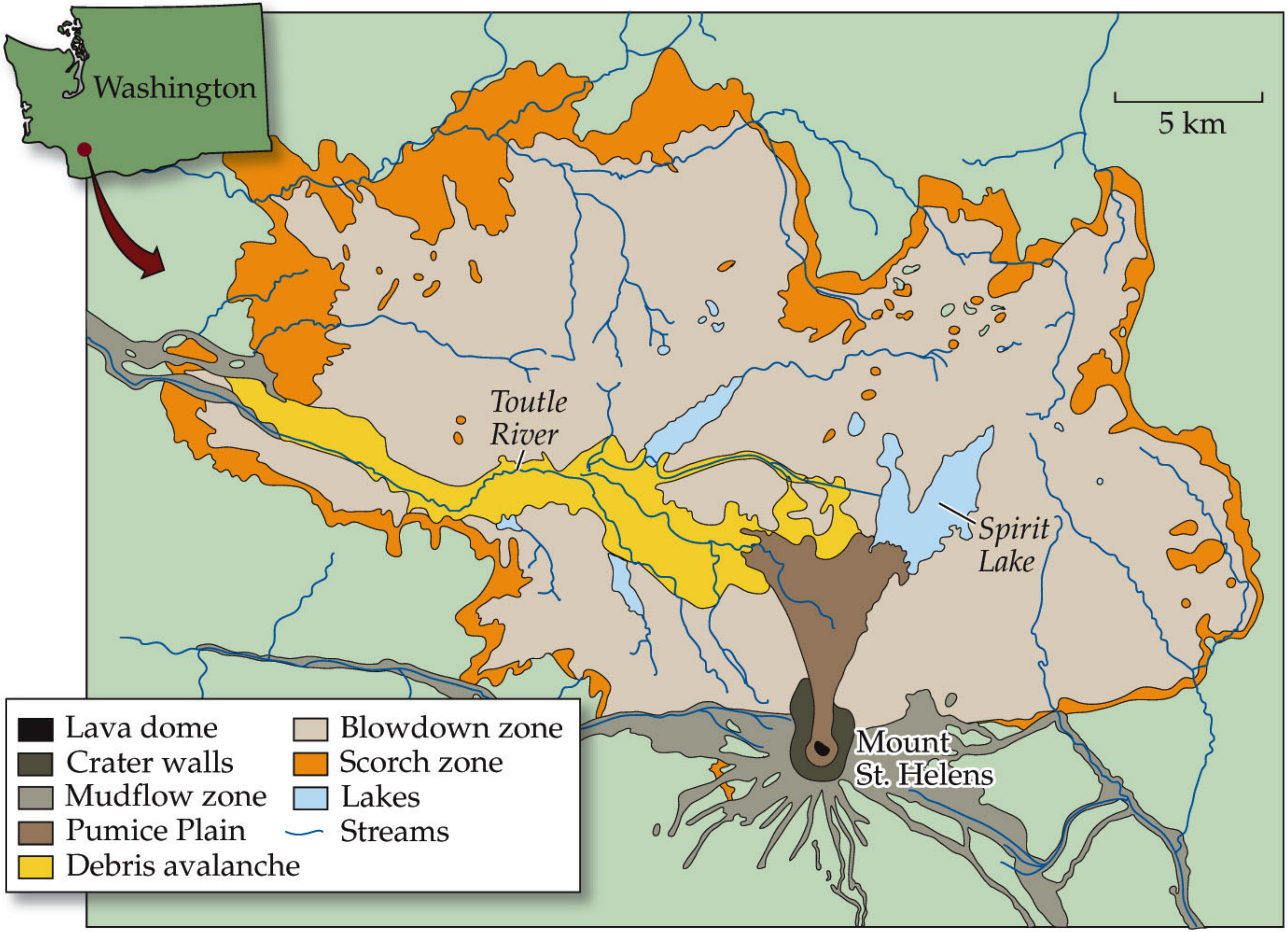
Devastation created new habitats devoid of any living organisms.

Case Study: A Natural Experiment of Mountainous Proportions

The eruption resulted in avalanches, rock and mud flows, hot sterilizing pumice, hot air that burned forests to ash, blew down trees for miles, blanketed the landscape with ash, filled Spirit Lake with debris and killed all aquatic life.

In many places, there was no organic matter left.

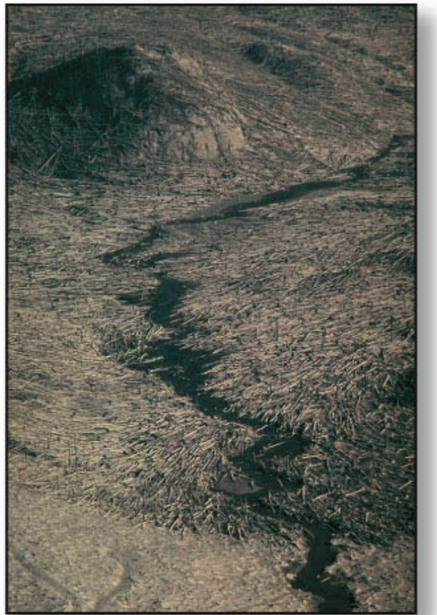
Figure 16.2 A Transformed Mount St. Helens (Part 1)



ECOLOGY, Figure 16.2 (Part 1)

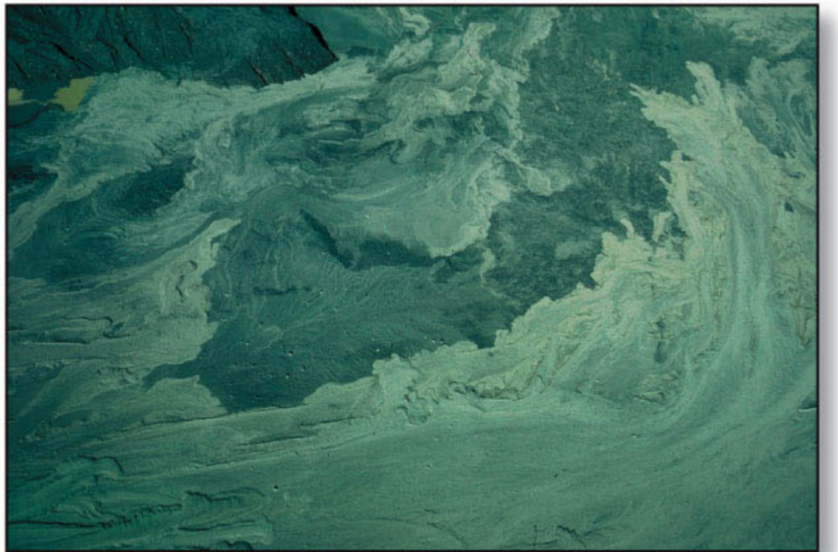
Figure 16.2 A Transformed Mount St. Helens (Part 2)

Blowdown zone



Scorch zone

Debris avalanche



Pumice Plain

ECOLOGY, Figure 16.2 (Part 2)

Case Study: A Natural Experiment of Mountainous Proportions

Almost immediately, scientists arrived to study this “natural experiment.”

They were able to document the sequence of biological changes that started soon after the eruption.

Much of what has been learned has been unexpected, and has changed the way we view the recovery of communities and the persistence of life on Earth.

Introduction

Communities are always changing, some more than others.

Human actions are becoming one of the strongest forces behind community change, and we have an imperfect understanding of the consequences of those actions.

Concept 16.1: Agents of change act on communities across multiple temporal and spatial scales.

Consider a coral reef community in the Indian Ocean.

If you could look back at it over the last few decades, you would observe slow and subtle changes, as well as catastrophic ones.

Agents of Change

Catastrophic changes includes massive coral death due to bleaching events (loss of symbiotic algae).

And the great tsunami of 2004, resulting in the replacement of some coral species with other species, or no replacement at all.

Succession is the change in species composition in communities over time.

It is the result of both biotic and abiotic factors.

Abiotic factors, in the form of climate, soils, nutrients, and water, vary over daily, seasonal, decadal, and even 100,000-year time scales.

In the Indian Ocean, unusually high water temperatures driven by large-scale climate change have been implicated in recent coral bleaching.

If symbiotic algae don't return, the corals die, creating conditions for species replacement.

Figure 16.3 Change Happens

ECOLOGY, Figure 16.3

Increases in sea level can decrease available light to corals and their symbionts.

This can lead to replacement by species tolerant of low light levels.

Because abiotic conditions are constantly changing, communities are doing the same.

Agents of Change

Abiotic agents of change can be put in two categories:

- **Disturbance**—an event that injures or kills some individuals and creates opportunities for other individuals (e.g., the 2004 tsunami killed or injured many individuals).
- **Stress**—an abiotic factor reduces the growth or reproduction of individuals (e.g., temperature increase).

TABLE 16.1

Examples of Abiotic and Biotic Agents of Change and Their Effects on Organisms

Agent of change	Effects	Habitats	Examples
ABIOTIC FACTORS			
Waves, currents	Organisms are detached, injured, or killed	Terrestrial, marine, freshwater	Storms, hurricanes, floods, tsunamis, ocean upwelling
Wind	Organisms are detached, injured, or killed	Terrestrial, marine, freshwater	Storms, hurricanes, wind-driven sediment scouring
Water supply	Organisms grow slowly, are injured, or are killed	Terrestrial, marine, freshwater	Droughts, floods, mudslides
Chemical composition	Organisms grow slowly, are injured, or are killed	Terrestrial, marine, freshwater	Pollution, acid rain, high or low salinity, high or low nutrients
Temperature	Organisms grow slowly, are injured, or are killed	Terrestrial, marine, freshwater	Freezing, snow and ice, avalanches, excessive heat, fire, sea level rise or fall
Volcanic activity	Organisms are injured or killed	Terrestrial, marine	Lava, hot gas, mudslides, flying rocks and debris, floods
BIOTIC FACTORS			
Negative interactions	Organisms grow slowly, are injured, or are killed	Terrestrial, marine, freshwater	Competition, predation, herbivory, disease, parasitism
Positive interactions	Organisms grow rapidly, less injury and death	Terrestrial, marine, freshwater	Mutualisms, commensalisms

Source: Adapted, with additions, from Sousa 2001.

Agents of Change

Both disturbance and stress are thought to play critical roles in succession.

Biotic interactions can also can result in the replacement of one species with another.

Ecosystem engineers or keystone species can also influence community change.

Agents of Change

Abiotic and biotic factors often interact to produce community change.

Example: An ecosystem engineer causes changes in abiotic conditions that can cause species replacement.

Beavers creating a wetland leads to species replacements.

Abiotic factors can alter species interactions.

Example: Drought condition alter the role of keystone species in northern California streams.

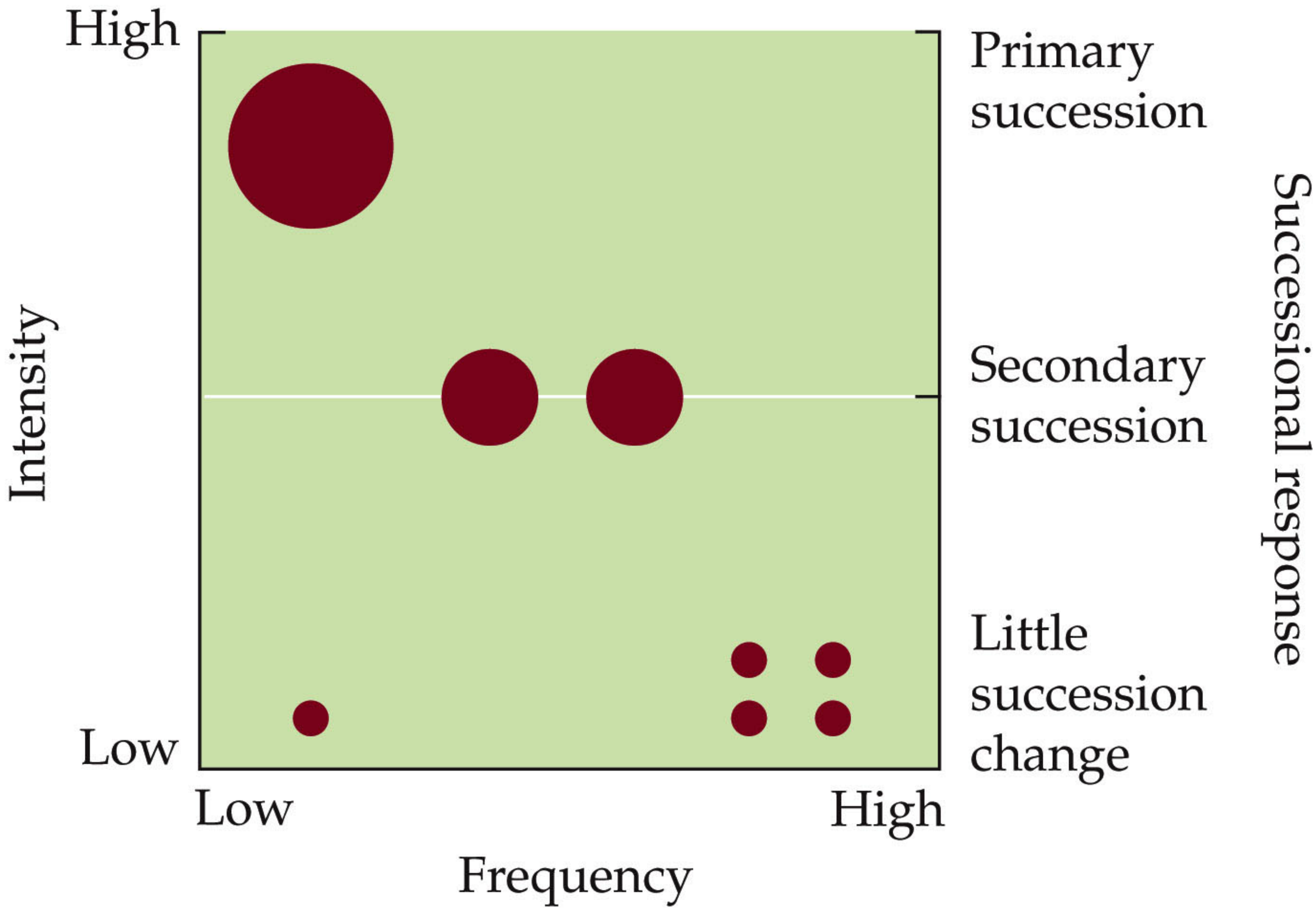
Agents of Change

Agents of change vary in frequency and magnitude.

The Mt. St. Helens eruption was huge, in both magnitude and area covered; but the frequency of this kind of disturbance is low.

At the other end of the spectrum are weak, frequent disturbances.

Figure 16.4 The Spectrum of Disturbance



Smaller and more frequent disturbances, such as a tree blowing down, can open patches of resources for other individuals.

A mosaic of disturbed patches can promote species diversity over time, but might not lead to much successional change.

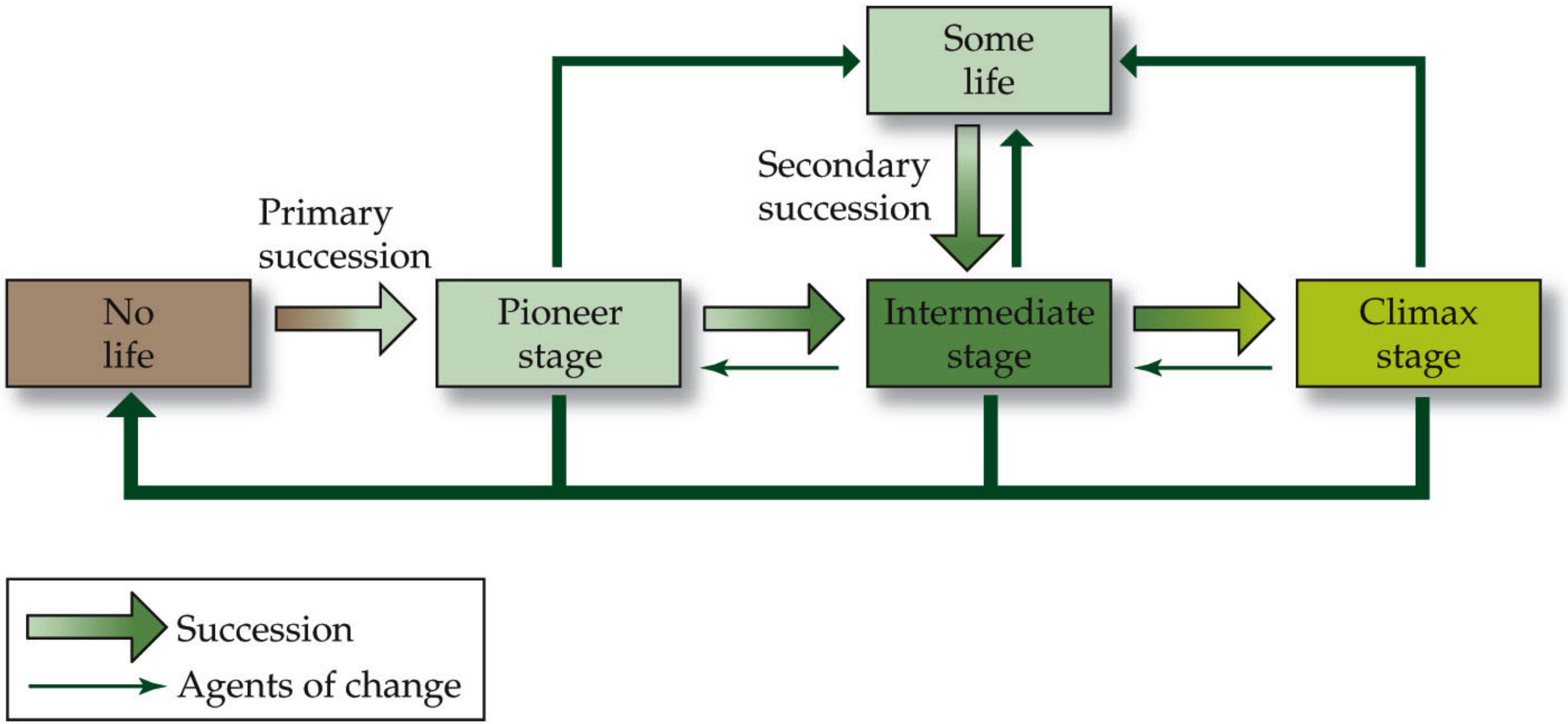
Concept 16.2: Succession is the change in species composition over time as a result of abiotic and biotic agents of change.

Studies of succession often focus on vegetative change, but the roles of animals, fungi, bacteria, and other microbes are equally important.

Theoretically, succession progresses through various stages that include a **climax stage**—a stable end point that experiences little change.

There is some argument about whether succession can ever lead to a stable end point.

Figure 16.5 A Theoretical Model of Succession



Basics of Succession

Two types of succession differ in their initial stage.

- **Primary succession** involves the colonization of habitats devoid of life (e.g., volcanic rock).
- **Secondary succession** involves reestablishment of a community in which some, but not all, organisms have been destroyed.

Basics of Succession

Primary succession can be very slow—the first arrivals face extremely inhospitable conditions.

The first colonizers tend to be species that can withstand stress and transform the habitat in ways that benefit their further growth and that of other species.

In secondary succession, the legacy of the preexisting species and their interactions with colonizing species play larger roles than in primary succession.

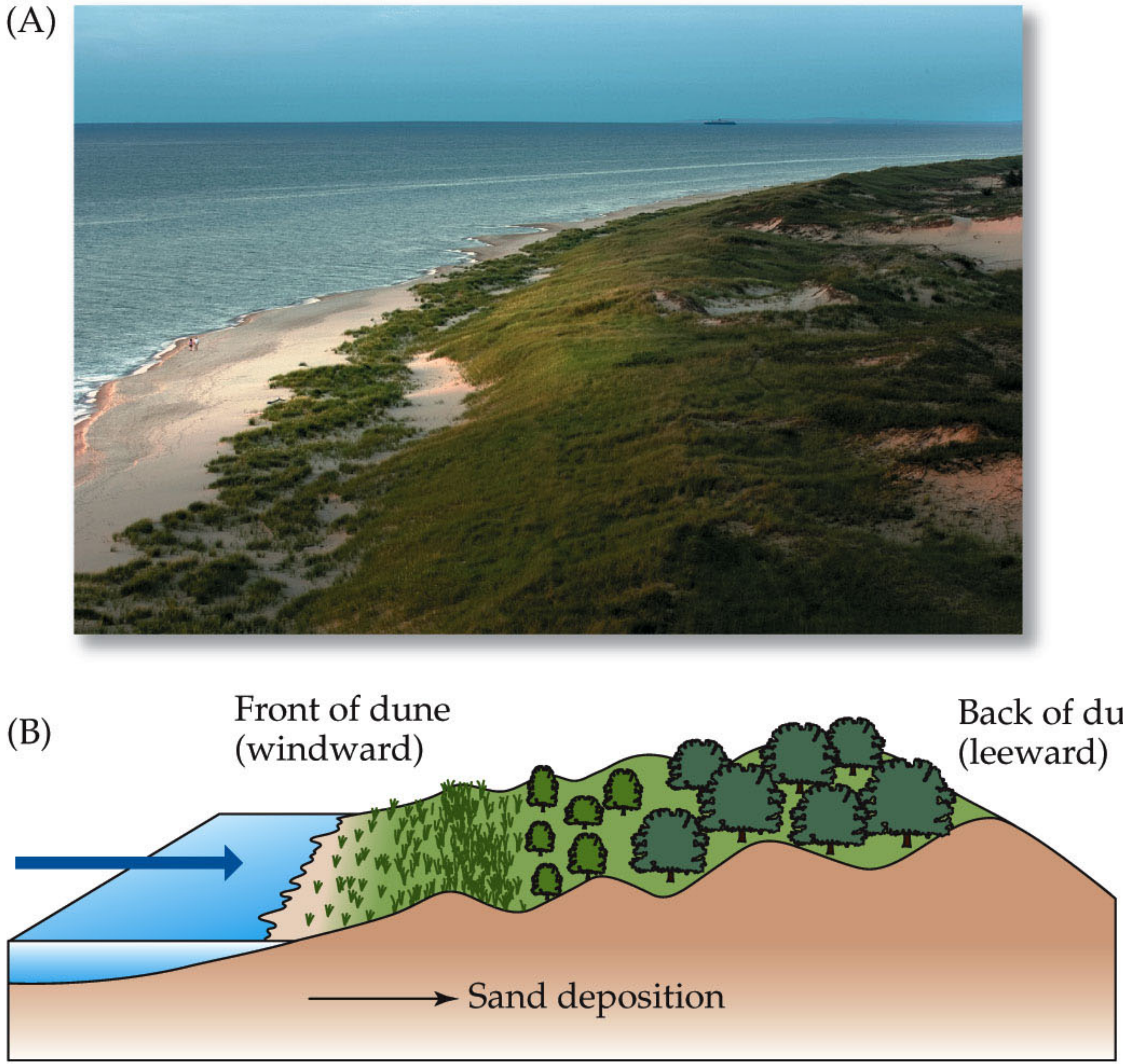
Basics of Succession

Modern ecology got its start by people interested in the succession of plant species.

Henry Cowles (1899) studied the successional sequence of vegetation on sand dunes along Lake Michigan.

He assumed that plant assemblages farthest from the lake's edge were the oldest; the ones nearest the lake were youngest.

Figure 16.6 Space for Time Substitution



Basics of Succession

Thus, Cowles could see successional stages arranged spatially.

This allowed him to predict how a community would change over time without actually waiting for the pattern to unfold, which would have taken decades to centuries.

This is called "space for time substitution" and is used frequently today.

Basics of Succession

The first stages were dominated by a hardy ecosystem engineer, American beach grass.

Beach grass traps sand and creates hills that provide refuge for plants less tolerant of constant burial and scouring.

Two other early ecologists:

- Frederick Clements believed plant communities were like “superorganisms,” groups of species working together toward some deterministic end.

Succession was similar to the development of an organism.

Basics of Succession

Clements felt that each community had a predictable life history and, if left undisturbed, ultimately reached a stable end point called the “climax community”.

The climax community was composed of dominant species that persisted over many years and provided stability that could be maintained indefinitely.

Basics of Succession

- Henry Gleason thought that communities were the random product of fluctuating environmental conditions acting on individual species.

Communities were not the predictable and repeatable result of coordinated interactions among species.

Basics of Succession

Clements and Gleason held the extreme views of succession.

Elements of both theories are found in the many successional studies carried out since then.

Charles Elton was influenced by these botanists, and also by his interest in animals.

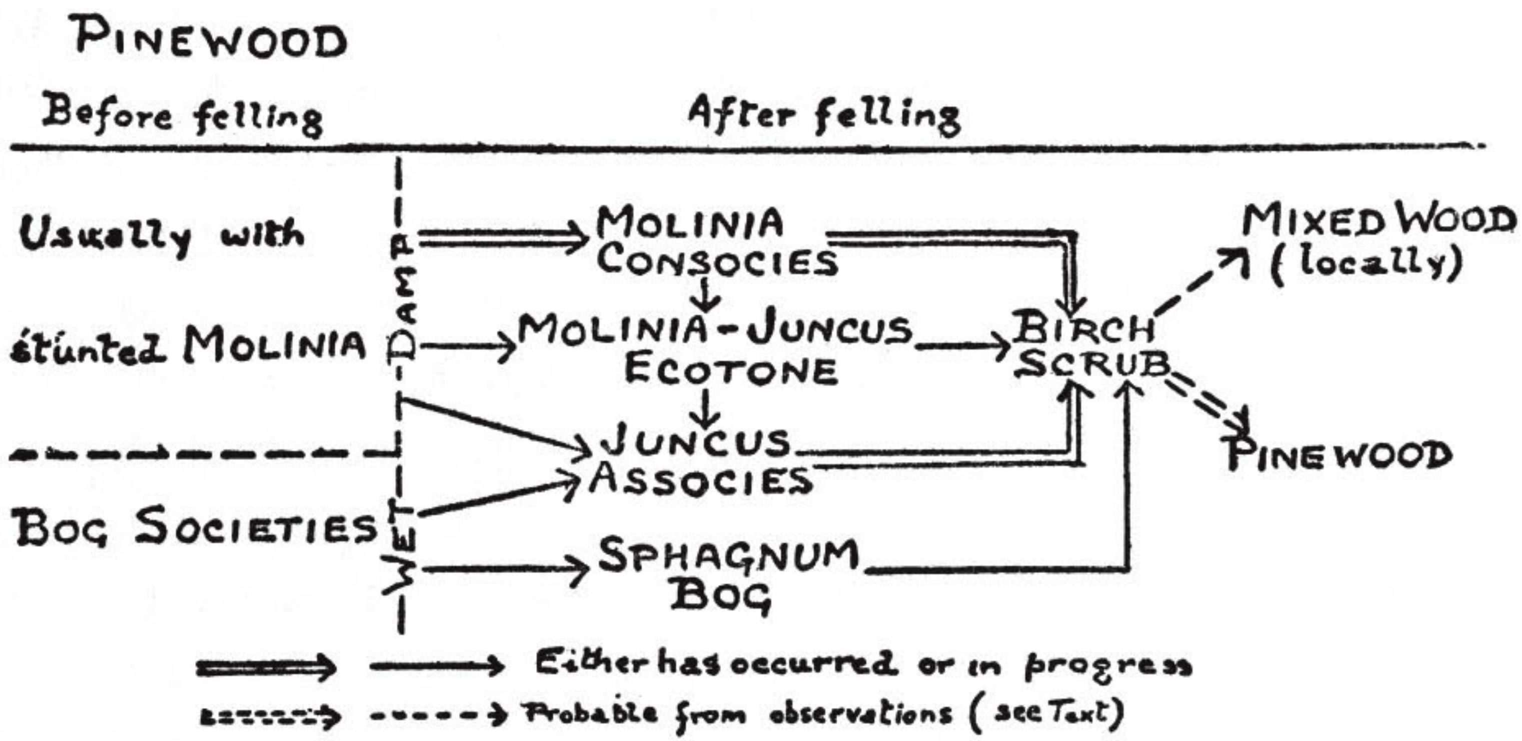
Basics of Succession

Elton believed that both organisms and the environment interact to shape the direction of succession.

In pine forests in England, the trajectory of succession following felling depended on moisture conditions. Wet areas developed into sphagnum bogs, drier areas developed into grass and sedge marshes.

Figure 16.7 B Elton's Trajectory of Pine Forest Succession

(B)



The two communities converged into birch scrub, but then diverged again.

Elton emphasized that the only way to predict the trajectory of succession was to understand the biological and environmental context in which it occurred.

Basics of Succession

Elton also recognized the contribution of animals to succession.

He showed how animals, by eating, dispersing, trampling, and destroying vegetation could greatly influence the sequence and timing of succession.

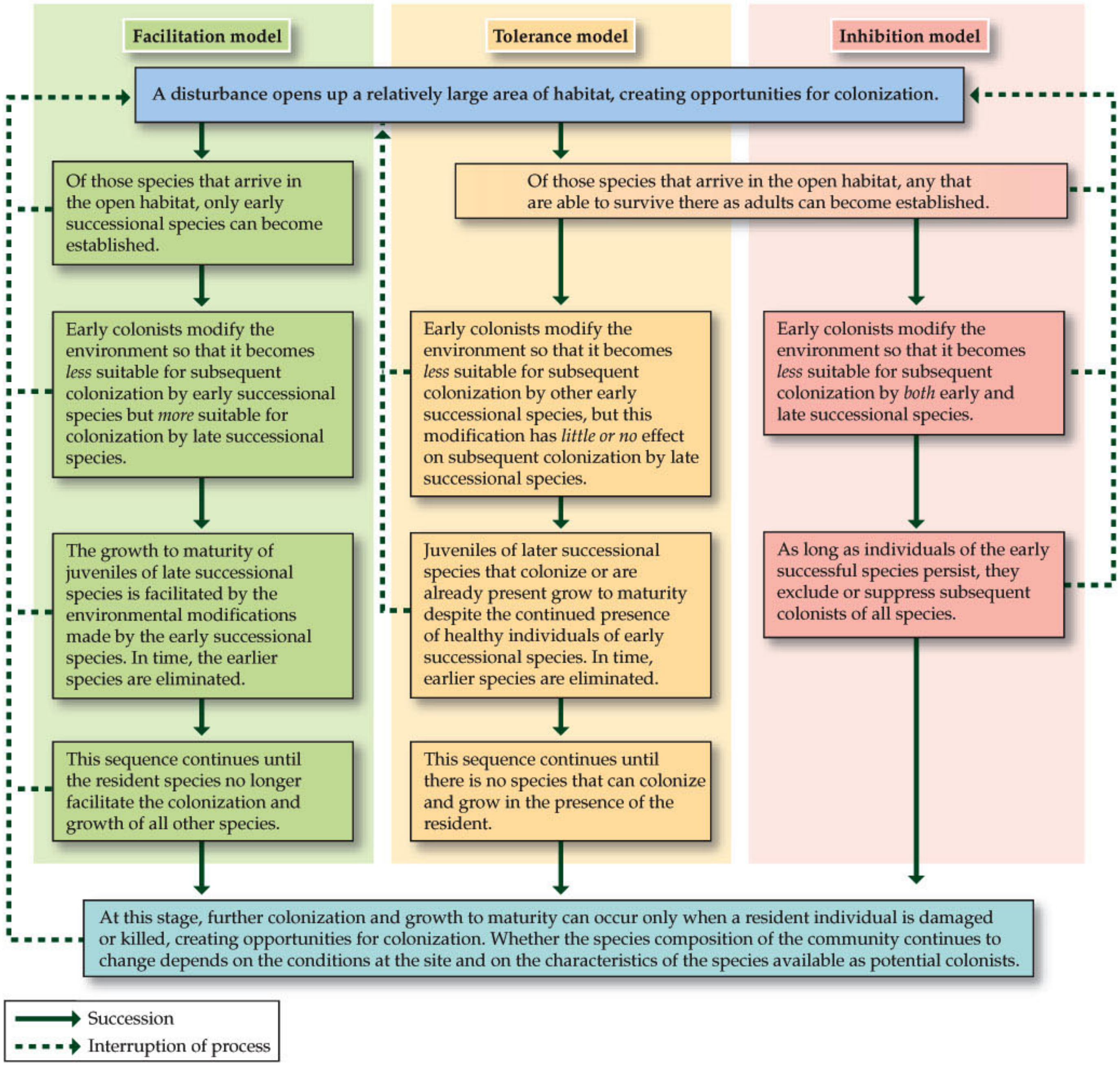
Connell and Slatyer (1977) reviewed the literature on succession and proposed three models:

- *Facilitation model*, inspired by Clements. Early species modify the environment in ways that benefit later species. The sequence of species facilitations leads to a climax community.

Basics of Succession

- *Tolerance model*—also assumes the earliest species modify the environment, but in neutral ways that neither benefit nor inhibit later species.
- *Inhibition model*—assumes early species modify conditions in negative ways that hinder later successional species.

Figure 16.8 Three Models of Succession



ECOLOGY, Figure 16.8

The role of animals is included in all three models.

Since the publication of this theoretical paper, many experimental tests of the models have been made.

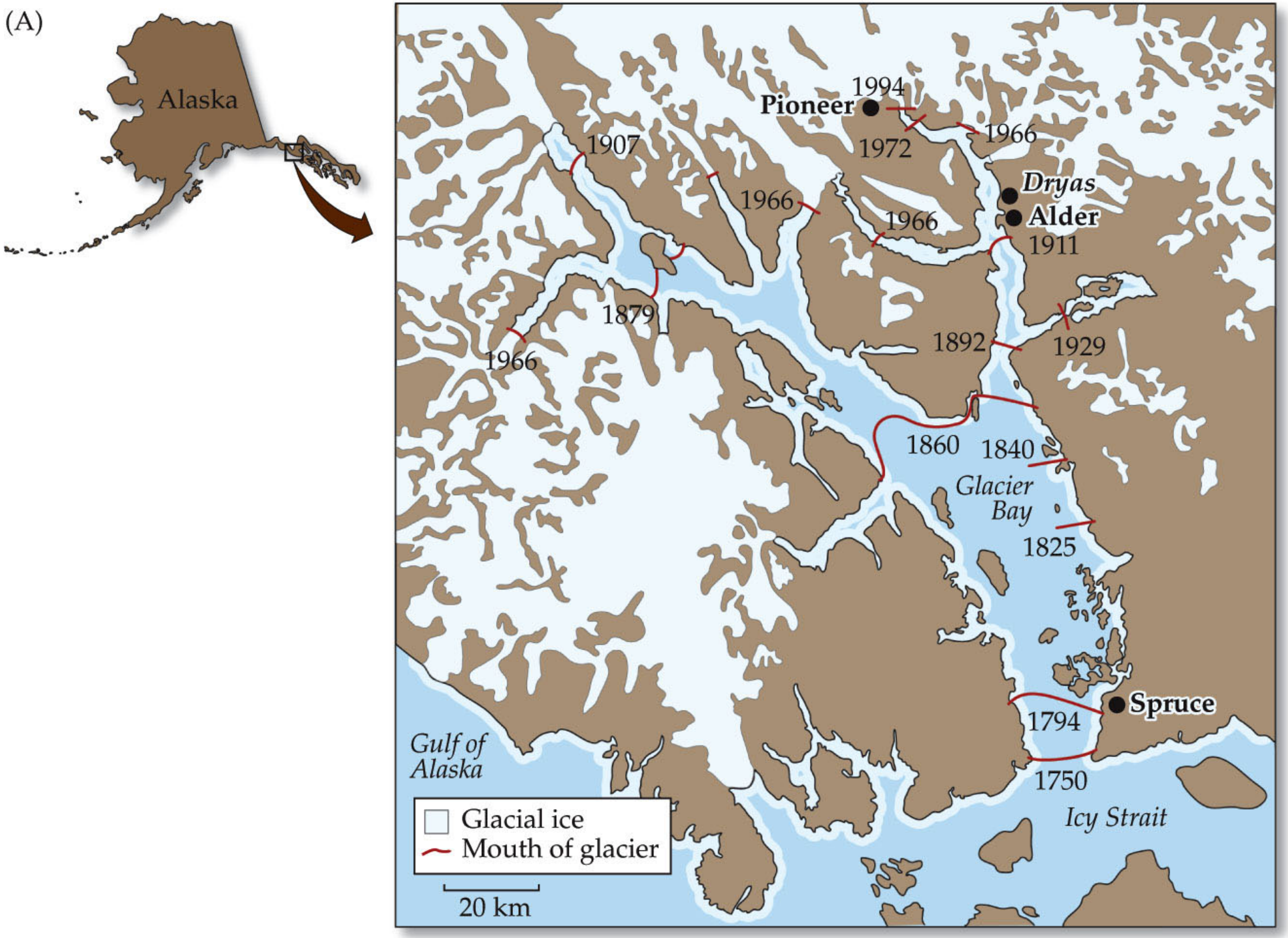
The mechanisms driving succession rarely conform to any one model, but are dependent on the community and the environmental context.

Concept 16.3: Experimental work on succession shows its mechanisms to be diverse and context-dependent.

Glacier Bay, Alaska is one of the best-studied examples of primary succession.

Melting glaciers have led to a sequence of communities that reflect succession over many centuries.

Figure 16.9 Glacial Retreat in Glacier Bay, Alaska (Part 1)



ECOLOGY, Figure 16.9 (Part 1)

Figure 16.9 Glacial Retreat in Glacier Bay, Alaska (Part 2)

(B)

ECOLOGY, Figure 16.9 (Part 2)

Mechanisms of Succession

William Cooper, a student of Cowles, began studies of Glacier Bay in 1915, seeing it as a “space for time” substitution opportunity.

He established permanent plots that are still being used today.

Mechanisms of Succession

The pattern of community change is characterized by increasing plant species richness and change in composition, with time and distance from the melting ice front.

In newly exposed habitat, a **pioneer stage** develops, dominated by lichens, mosses, horsetails, willows, and cottonwoods.

Mechanisms of Succession

After about 30 years, the *Dryas* community develops, named for a small shrub.

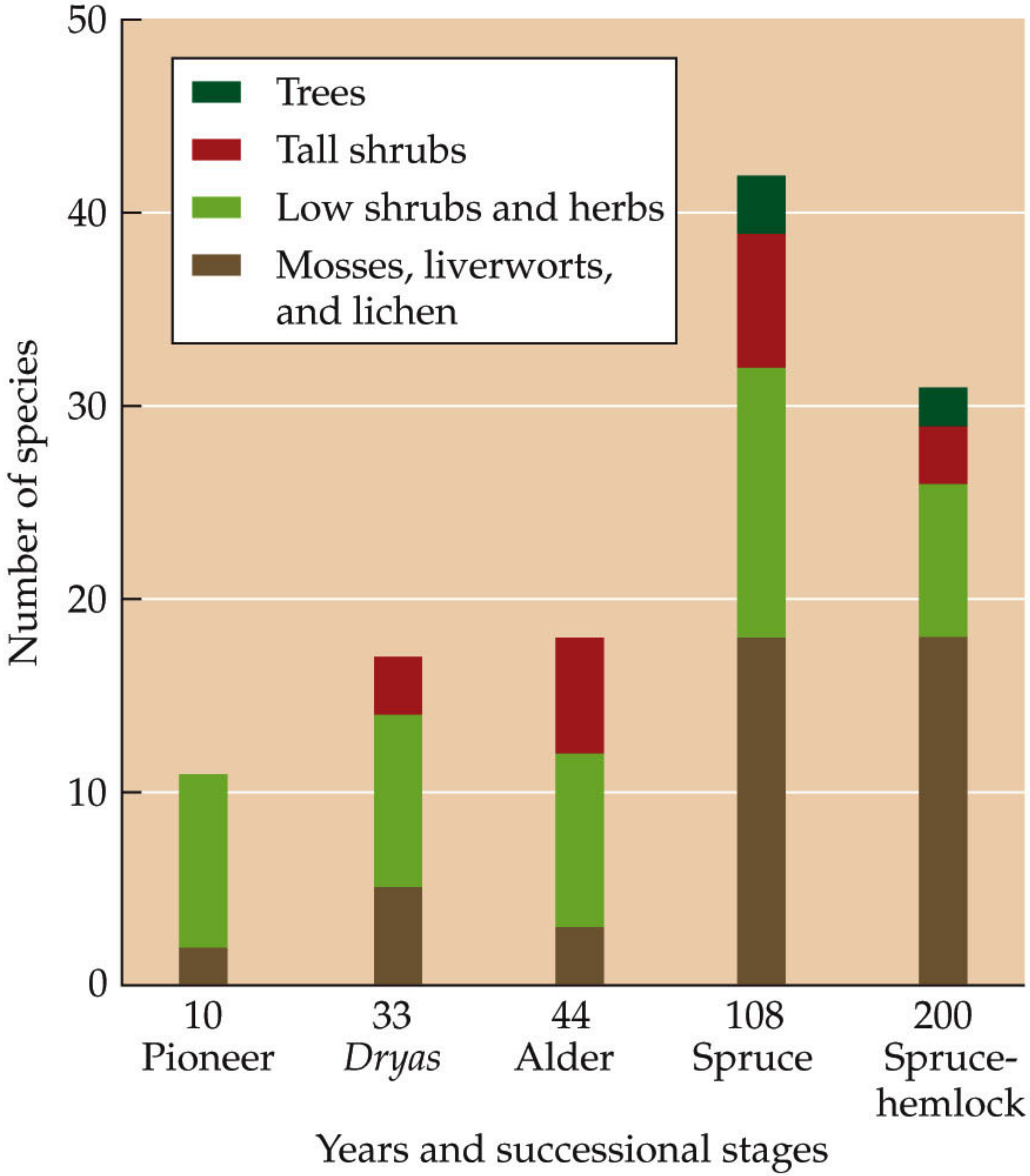
After about 50 years (or 20 km from the ice front), alders dominate, forming the alder stage.

100 years later, a mature Sitka spruce forest is in place.

Mechanisms of Succession

Two hundred years later, species richness decreases somewhat as Sitka spruce are replaced by Western hemlocks.

Figure 16.10 Successional Communities at Glacier Bay, Alaska



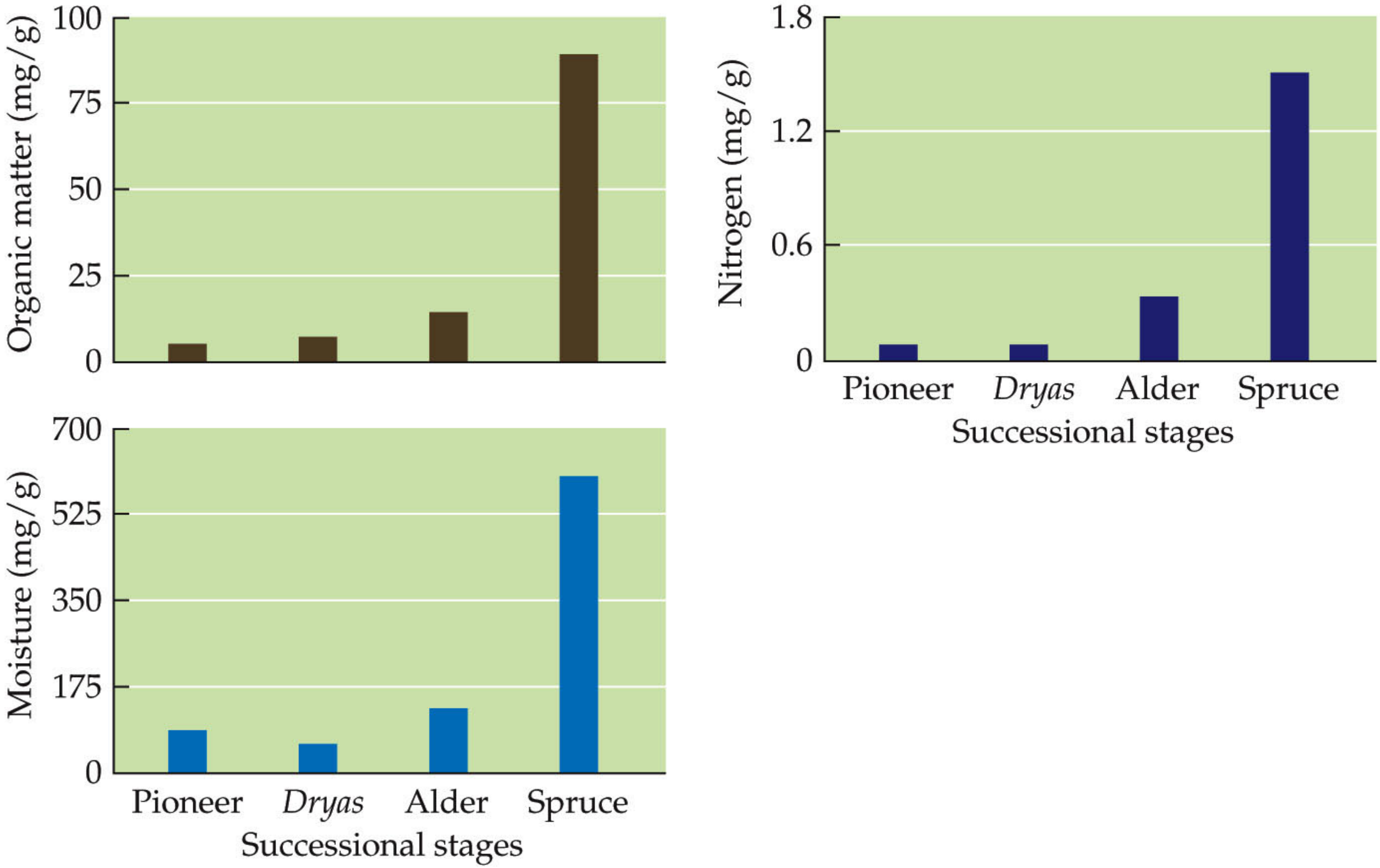
ECOLOGY, Figure 16.10

Mechanisms of Succession

Chapin et al. (1994) examined the mechanisms underlying this successional pattern.

They analyzed soils in various stages: Soil organic matter, moisture, and nitrogen concentration increased as plant species succession progressed.

Figure 16.11 Soil Properties Change with Succession



Mechanisms of Succession

In manipulative experiments, spruce seeds were added to each successional stage. Germination, growth, and survival were monitored over time.

Neighboring plants had both facilitative and inhibitory effects on the spruce seedlings, but the direction and strength of those effects varied with successional stage.

Figure 16.12 Both Positive and Negative Effects Influence Succession

Successional stages	Pioneer	*Dryas*	Alder	Spruce
Positive effects	Higher survival rate	Higher nitrogen level Higher growth rate	Higher soil organic matter Higher nitrogen level More mycorrhizae Higher growth rate	Higher germination rate
Negative effects	Lower germination rate	Lower germination rate Lower survival rate Higher seed predation and mortality rate	Lower germination rate Lower survival rate Higher seed predation and mortality rate Root competition Light competition	Lower survival rate Higher seed predation and mortality rate Root competition Light competition Lower nitrogen level

Mechanisms of Succession

- Pioneer stage—spruce seedlings had low germination rate; higher survival rate.
- *Dryas* stage—increase in seed predators led to weak germination and survival; but survivors had better growth. *Dryas* has N-fixing bacteria.

Mechanisms of Succession

- Alder stage—more nitrogen (alders also have N-fixing bacteria) and soil organic matter produced positive effects; shading and seed predators led to overall poor germination and survival rates.

Mechanisms of Succession

- Spruce stage—effects of large spruce were mostly negative. Growth and survival rates were low due to competition with adult spruce for light, space, and nitrogen.

Mechanisms of Succession

Glacier Bay illustrated some of the mechansims of Connell and Slatyer's models:

- Early stages showed aspects of the facilitation model—plants modified the habitat in positive ways for other plants and animals.
- Later, species such as alders had negative effects on later successional species.

Mechanisms of Succession

- In the spruce stage, where dominance was an artifact of slow growth and long life, succession was driven by life history characteristics, a signature of the tolerance model.

Mechanisms of Succession

Salt marshes are characterized by different species compositions and physical conditions at different tidal elevations.

Cordgrass *Spartina patens* dominates near the sea border; spike rush *Juncus gerardii* is found at the terrestrial border.

Mechanisms of Succession

A common disturbance is tidal deposition of wrack (dead plant material) that smothers and kills plants, leaving patches where secondary succession occurs.

Salinity in the bare patches is high because of evaporation.

Figure 16.13 Wrack Creates Bare Patches in Salt Marshes

Mechanisms of Succession

The early successional species spike grass, *Distichlis spicata*, colonizes first.

It is eventually outcompeted by both *Spartina* and *Juncus* in their respective zones.

Bertness and Shumway (1993) manipulated patches after they had been colonized.

In the *Spartina* zone they removed *Distichlis* from half the patches, leaving *Spartina*, and removed *Spartina* from the other half, leaving *Distichlis*.

The same manipulation was done in the *Juncus* zone.

Mechanisms of Succession

Half of the patches were watered with fresh water to reduce salt stress.

The patches were observed for two years.

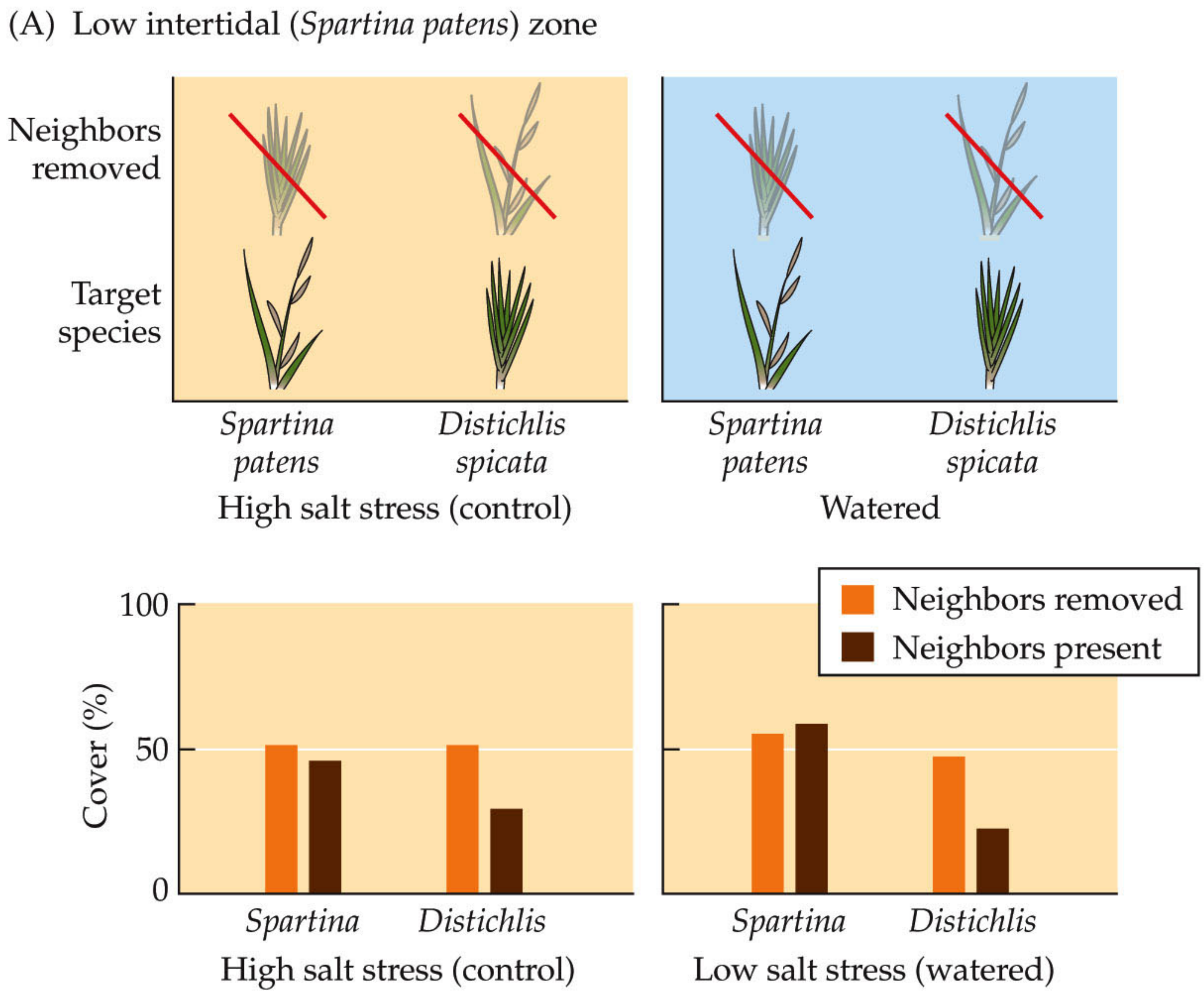
Mechanisms of succession varied depending on the level of salt stress and the species interactions involved.

Mechanisms of Succession

In the *Spartina* zone, *Spartina* always colonized and dominated the plots, whether or not *Distichlis* was present or watering occurred.

Distichlis was able to dominate only if *Spartina* was removed, so it was clearly inhibited by *Spartina.*

Figure 16.14 A New England Salt Marsh Succession Is Context-Dependent



ECOLOGY, Figure 16.14 (Part 1)

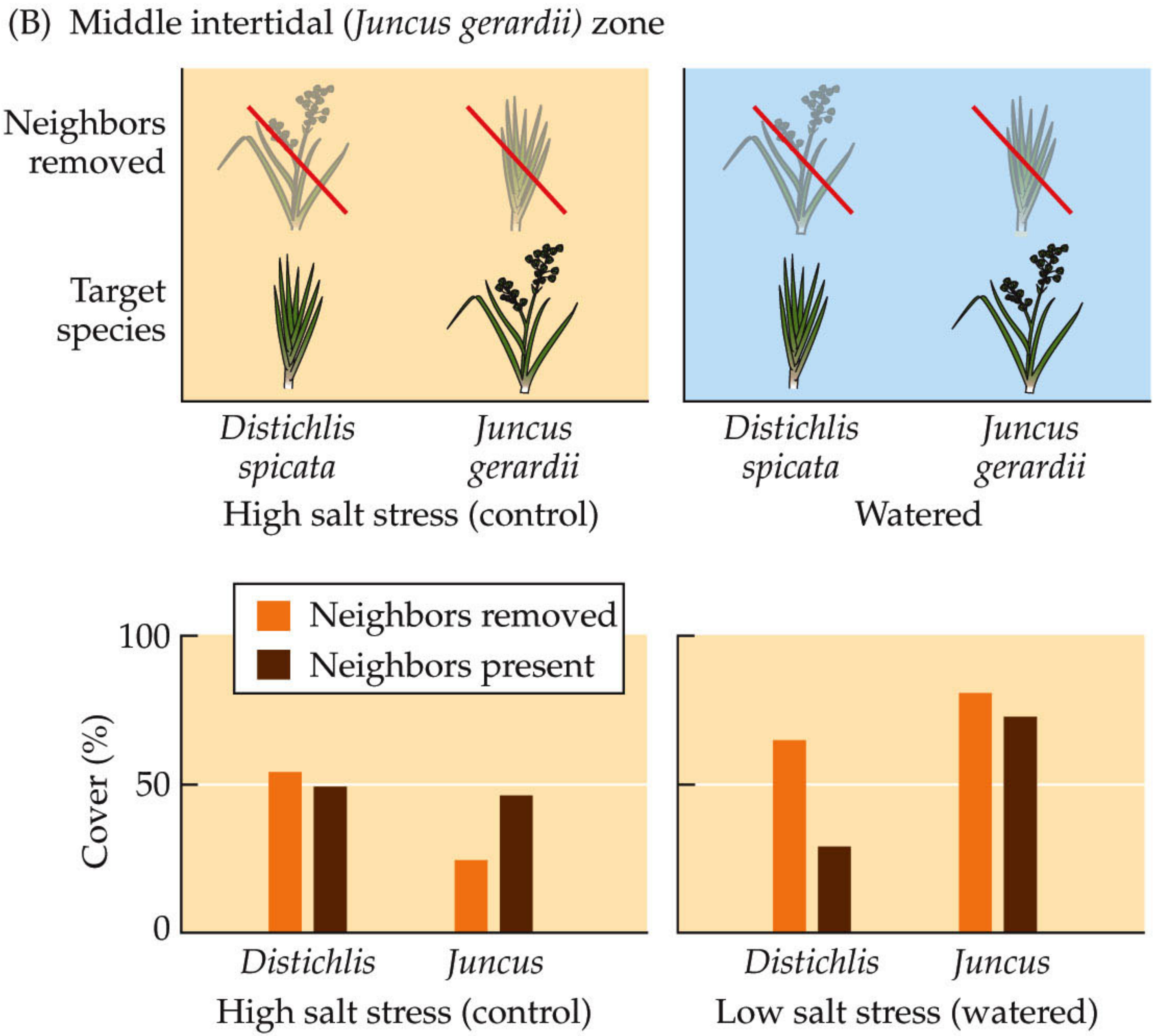
Mechanisms of Succession

In the Juncus zone, *Juncus* was able to colonize only if *Distichlis* was present or watering occurred.

The presence of *Distichlis* helped shade the soil surface, thus decreasing salt accumulation.

If plots were watered, *Distichlis* was easily outcompeted by *Juncus*.

Figure 16.14 B New England Salt Marsh Succession Is Context-Dependent



***ECOLOGY*, Figure 16.14 (Part 2)**

Mechanisms of Succession

Another community in which succession has been studied extensively is the rocky intertidal zone.

Disturbance is created mostly by storms—waves and debris rip out organisms.

Low tides expose organisms to high or low temperatures which can kill them or cause them to detach.

Mechanisms of Succession

In southern California, algae growing on boulders was disturbed every time boulders were overturned by waves.

Mechanisms of Succession

Sousa (1979) studied succession on the boulders. The first to colonize was always the seaweed *Ulva lactuca.*

It was followed by a red alga, *Gigartina canaliculata*.

In experiments on concrete blocks, he found that colonization by *Gigartina* could be accelerated if *Ulva* was removed.

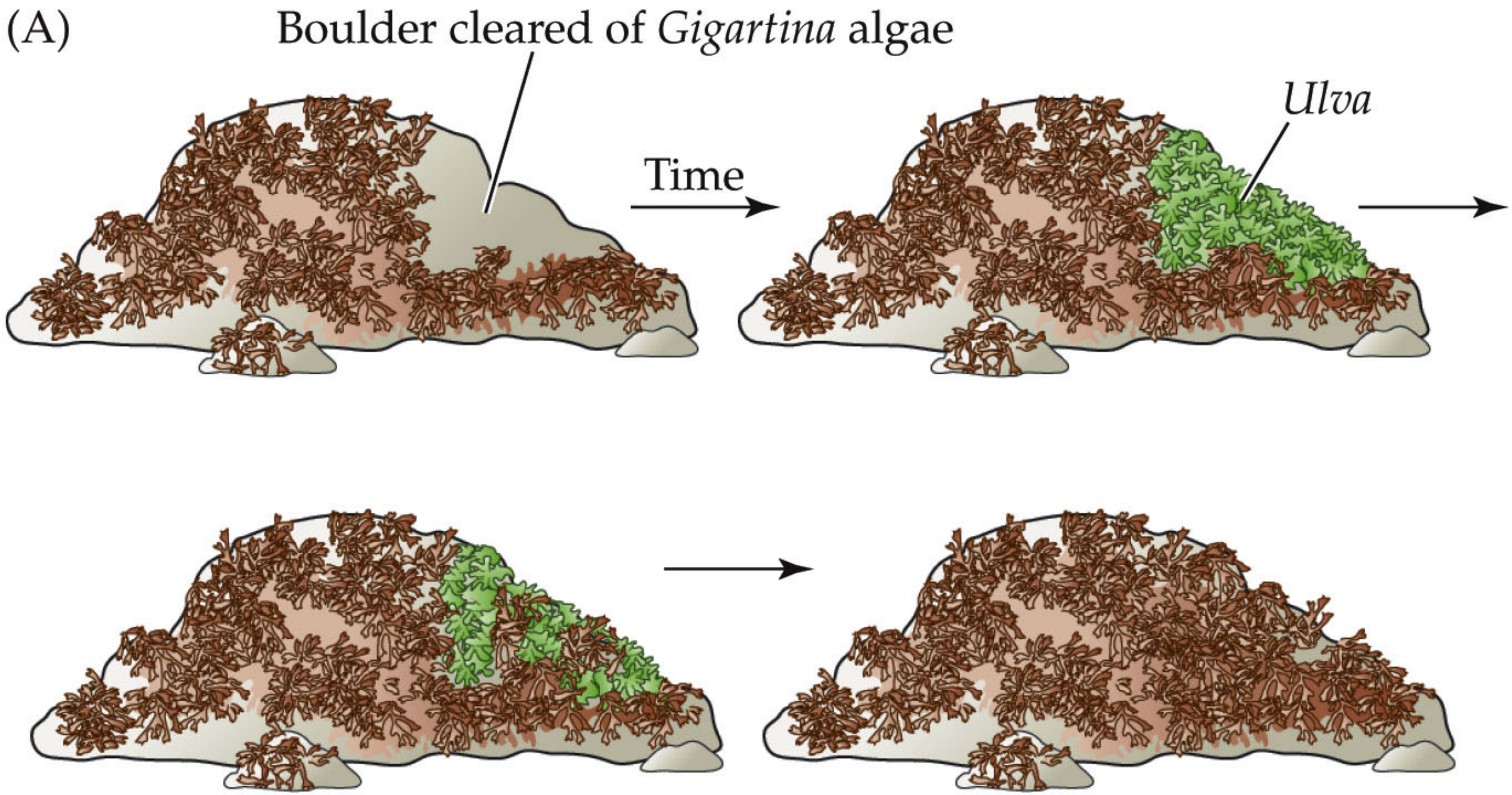

(A)
Boulder cleared of *Gigartina* algae
Time
Ulva

Figure 16.15 Algal Succession on Southern California Boulders Is Driven by Inhibition (Part 2)

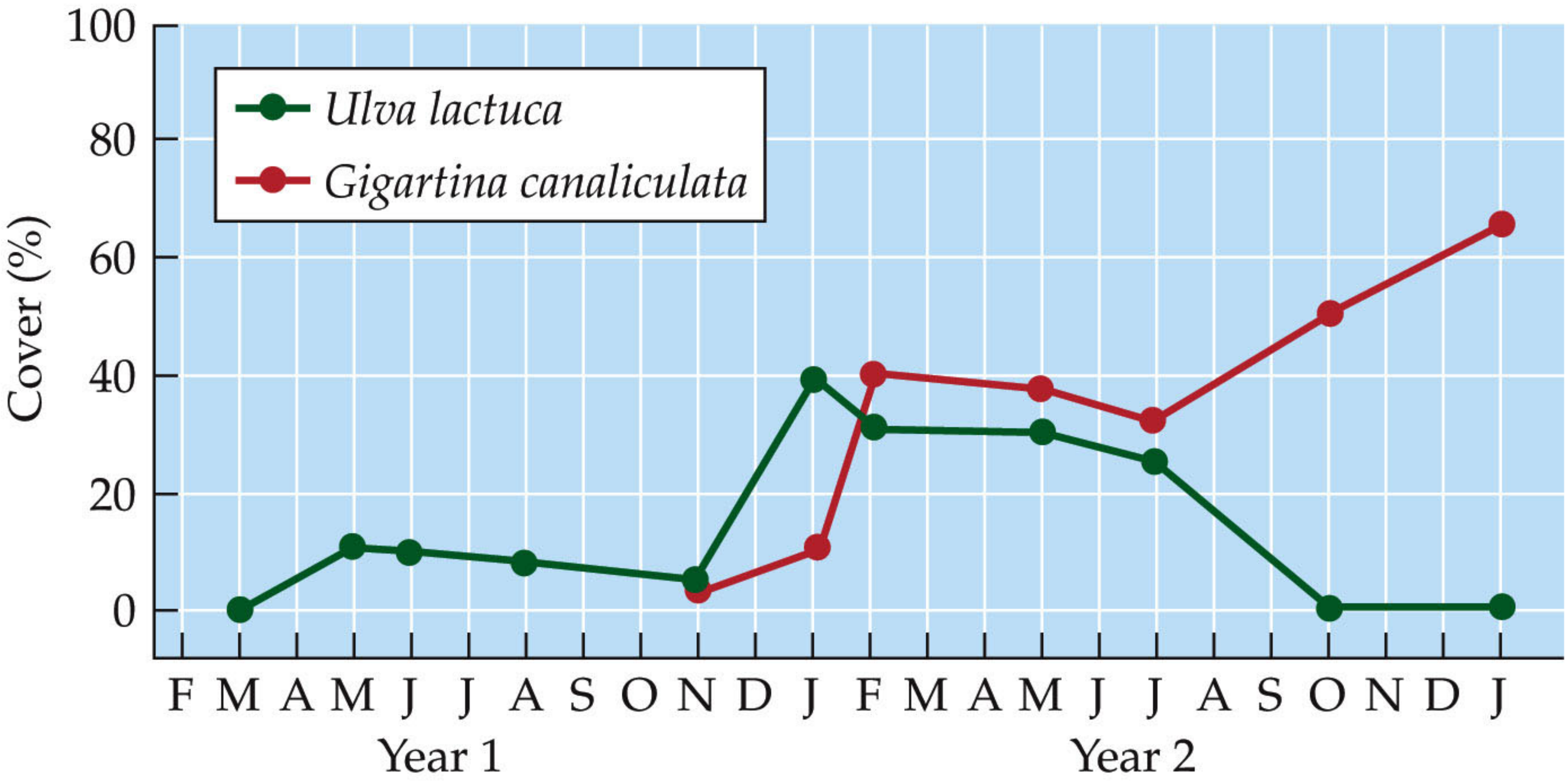
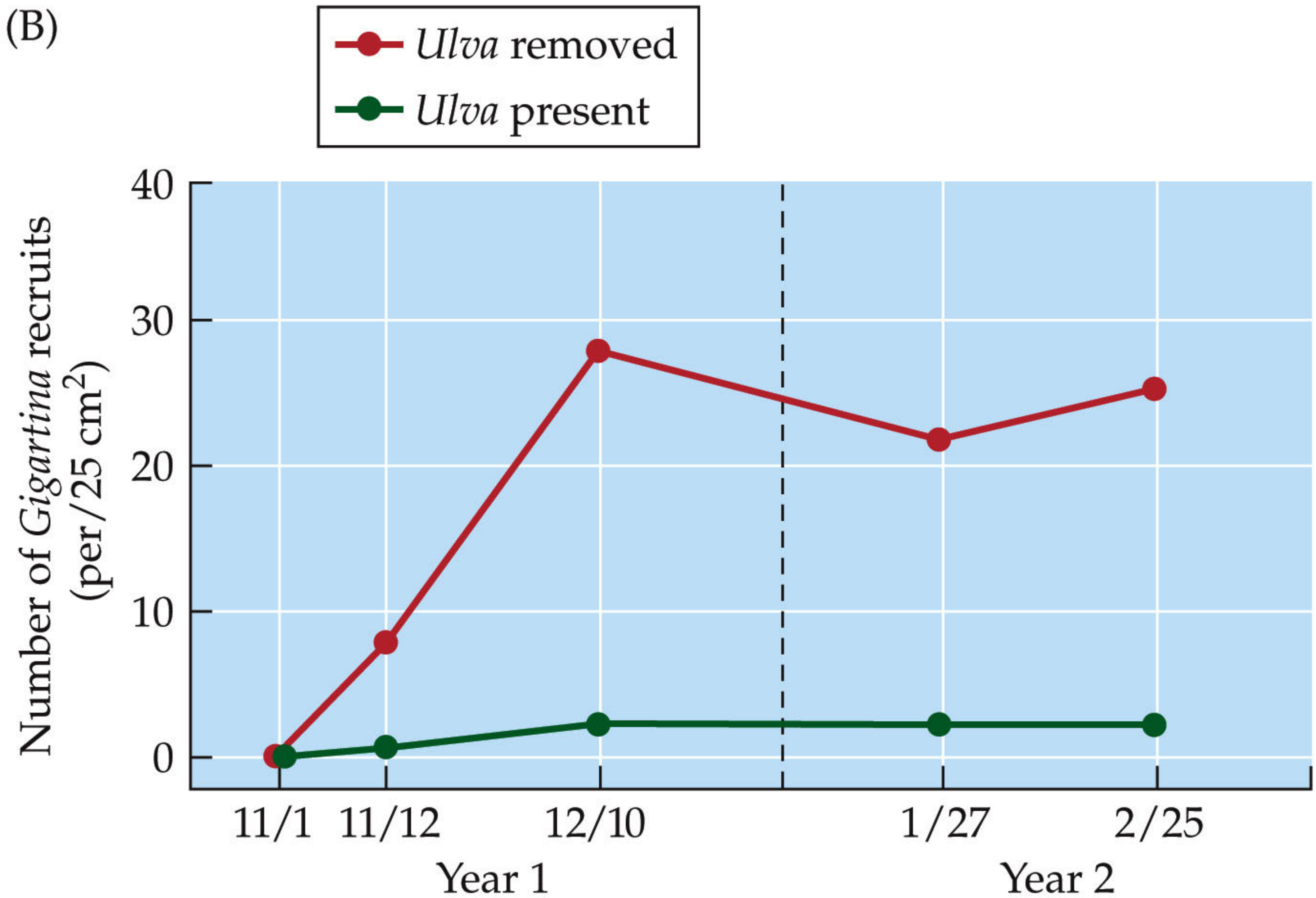


Figure 16.15 Algal Succession on Southern California Boulders Is Driven by Inhibition (Part 3)



ECOLOGY, Figure 16.15 (Part 3)

Mechanisms of Succession

If *Ulva* is able to inhibit other seaweed species, why doesn't it always dominate?

More experiments showed that grazing crabs preferentially fed on *Ulva*, thus initiating transition from the early *Ulva* stage to mid-successional red algal species.

Mechanisms of Succession

In turn, the mid-successional species were more susceptible to stress and epiphytes than the late successional *Gigartina*.

Gigartina dominated because it was the least susceptible to stress and herbivores.

Mechanisms of Succession

Succession in the rocky intertidal zone seemed to be driven by inhibition.

Facilitation and tolerance were thought to be much less important in a system where competition for space was the main driving factor.

Mechanisms of Succession

On the Oregon coast, the communities include many more sessile invertebrates, such as barnacles and mussels.

Farrell (1991) found that the first colonizer of bare patches was a barnacle, *Chthamalus dalli*, which was replaced by a larger barnacle species, *Balanus glandula*, which was replaced by three species of macroalgae.

Mechanisms of Succession

Removal experiments showed that *Chthamalus* did not inhibit *Balanus*, but *Balanus* was able to outcompete *Chthamalus* over time, thus supporting the tolerance model.

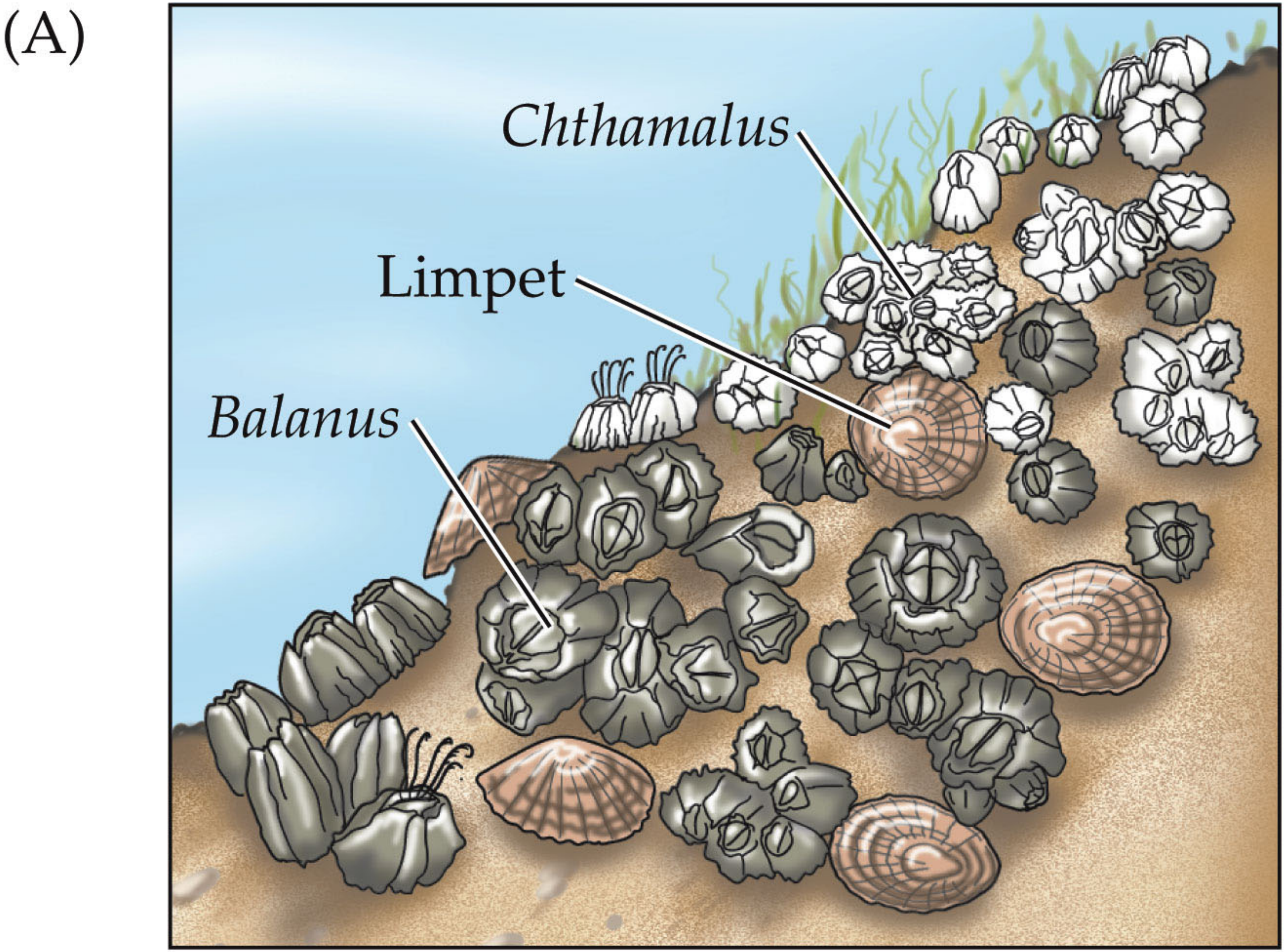
Balanus facilitated colonization by macroalgae, lending credibility to the facilitation model.

Farrell created experimental plots from which *Balanus*, limpets, or both were removed.

Macroalgae colonized all the plots without limpets, but had a much higher density in the plots with barnacles than in those without barnacles.

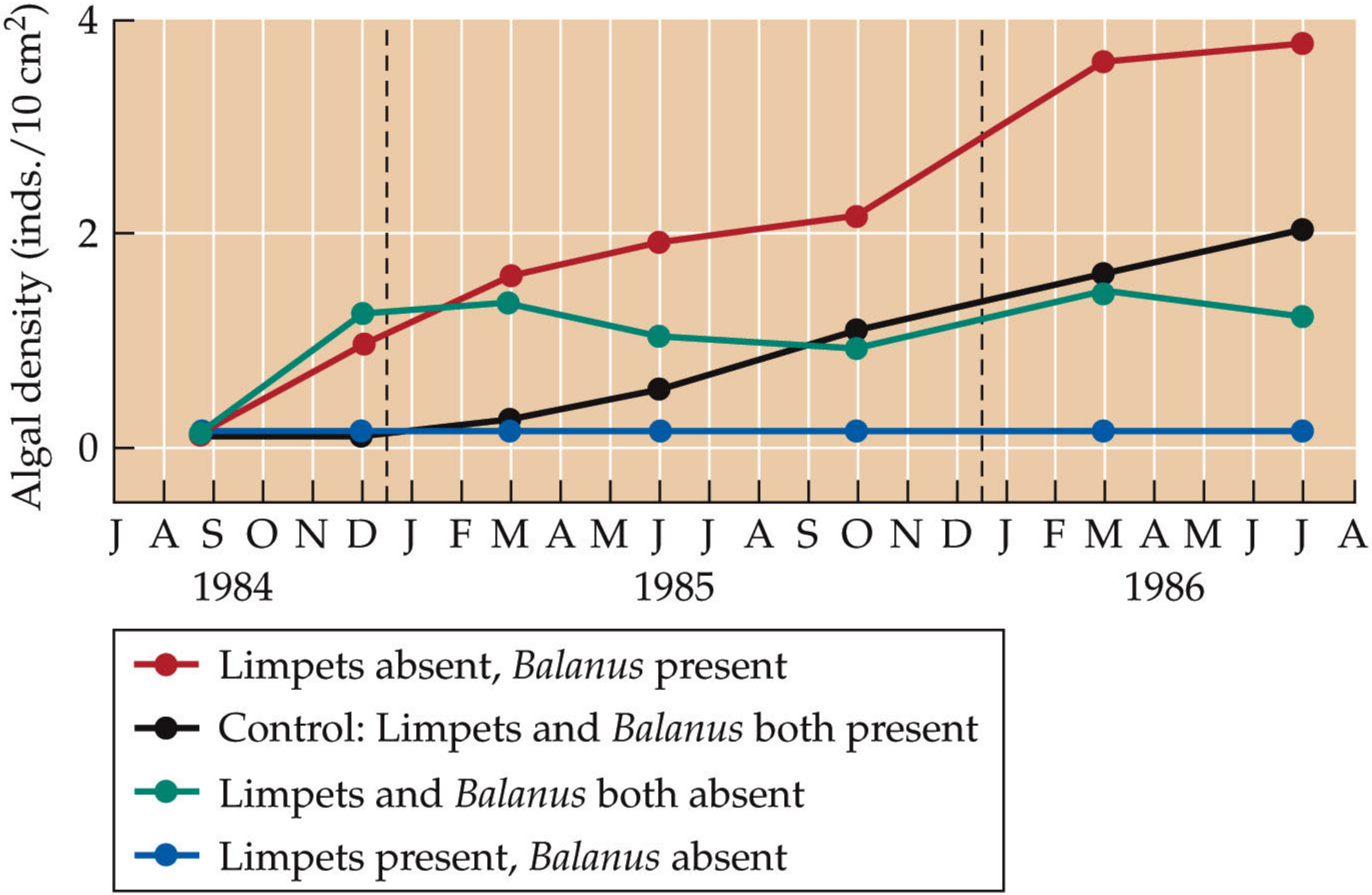
This suggested that *Balanus* kept limpets from grazing on newly settled macroalgal.

Figure 16.16 A Algal Succession on the Oregon Coast Is Driven by Facilitation (Part 1)



ECOLOGY, Figure 16.16 (Part 1)

Figure 16.16 A Algal Succession on the Oregon Coast Is Driven by Facilitation (Part 2)



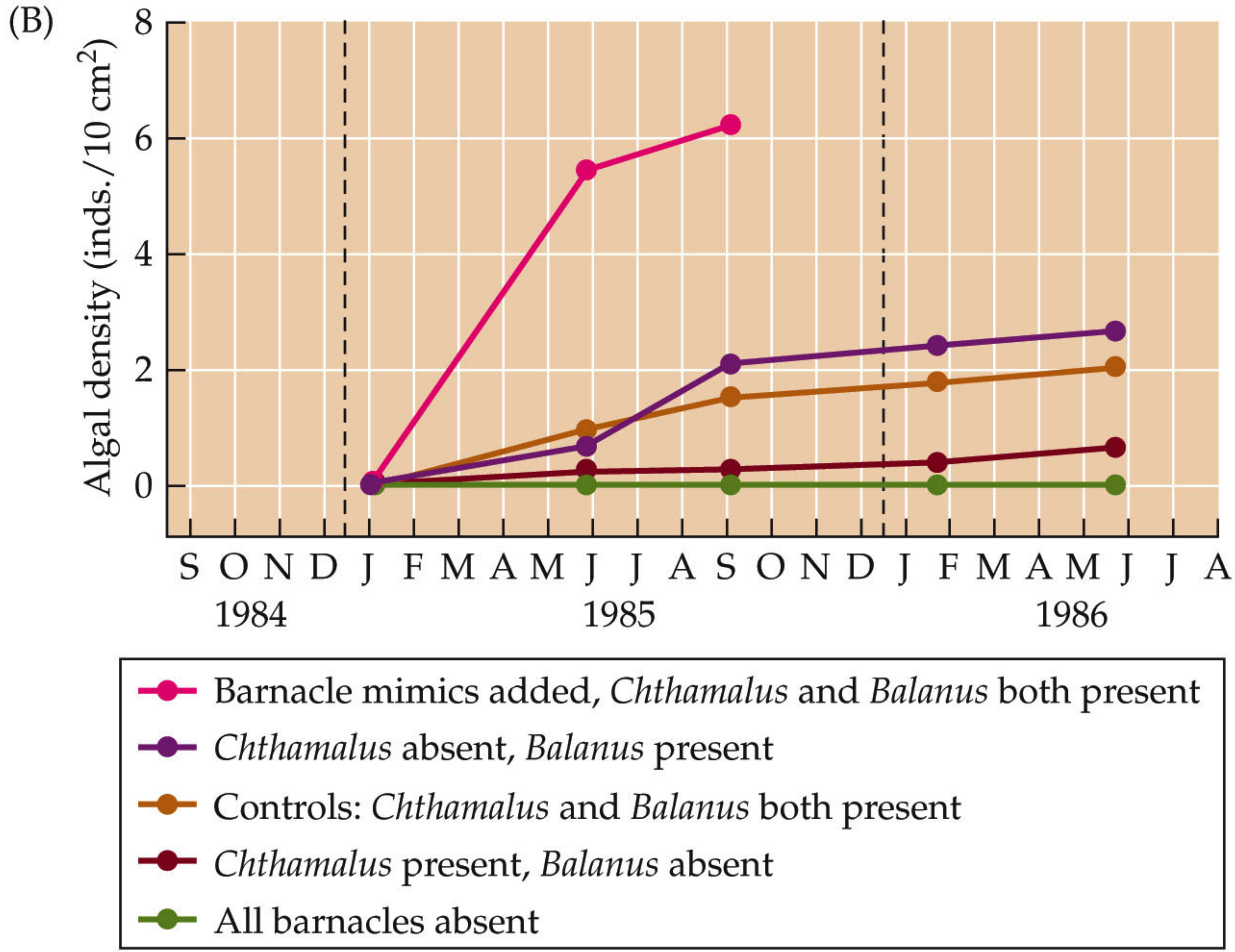
Mechanisms of Succession

Why doesn't *Chthamalus* have the same facilitative effect on macroalgae?

Ferrell suspected the reason was *Balanus*'s larger size.

Plaster casts similar to barnacles but larger than *Balanus* had a more positive effect on macroalge than smaller-sized live barnacles of either species.

Figure 16.16 B Algal Succession on the Oregon Coast Is Driven by Facilitation



ECOLOGY, Figure 16.16 (Part 3)

Mechanisms of Succession

Many experimental studies show that succession is driven by many mechanisms. No one model fits any one community.

Facilitative interactions are often important drivers of early succession, especially when physical conditions are stressful.

Mechanisms of Succession

As succession progresses, larger, slow-growing and long-lived species begin to dominate.

Competition probably plays a more dominant role than facilitation later in succession.

In mid- to late successional stages, an array of both positive and negative interactions are operating.

Concept 16.4: Communities can follow different successional paths and display alternative states.

In some cases different communities develop in the same area under similar environmental conditions—**alternative stable states**.

Alternative Stable States

A community is thought to be **stable** when it returns to its original state after some perturbation.

The stability of a community partly depends on the scale of observation, both spatially and temporally.

Ecologists have done much research on alternative stable states.

Sutherland (1974) studied marine fouling communities (sponges, hydroids, etc.) that grow on ships, docks, etc.

He suspended ceramic tiles from a dock and allowed them to be colonized by invertebrates.

After two years, tiles that had been put out in early spring were dominated by *Styela*, a solitary tunicate.

Other invertebrates were unable to colonize tiles already dominated by *Styela*; this was considered a stable state.

Tiles put out late in the summer were dominated by by *Schizoporella*, an encrusting bryozoan. Other species, including *Styela*, were unable to colonize these tiles.

In the next experiments, Sutherland excluded fish predators from half the tiles.

After a year, the tiles protected from fish predation had *Styela*-dominated communities, while those exposed to fish predation had *Schizoporella*-dominated communities.

(A)

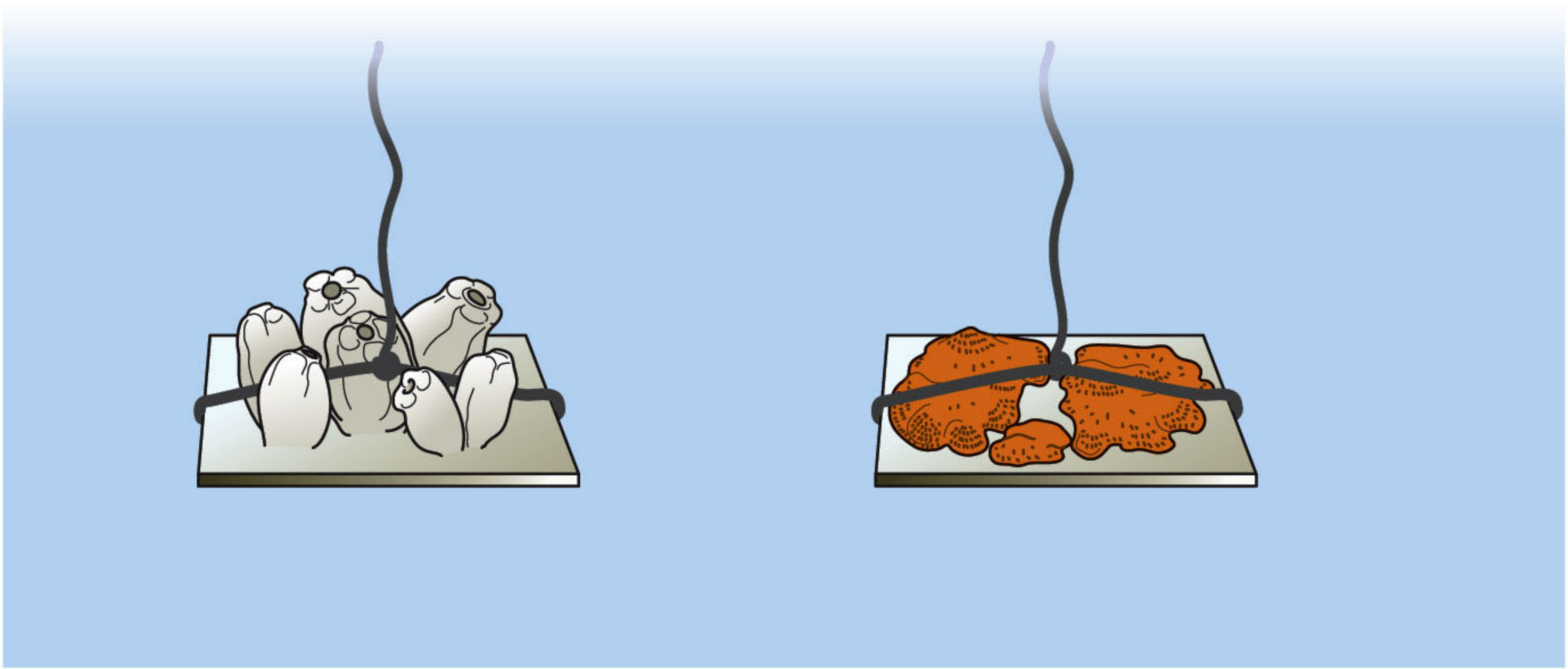


Figure 16.17 Fouling Communities Show Alternative States (Part 2)

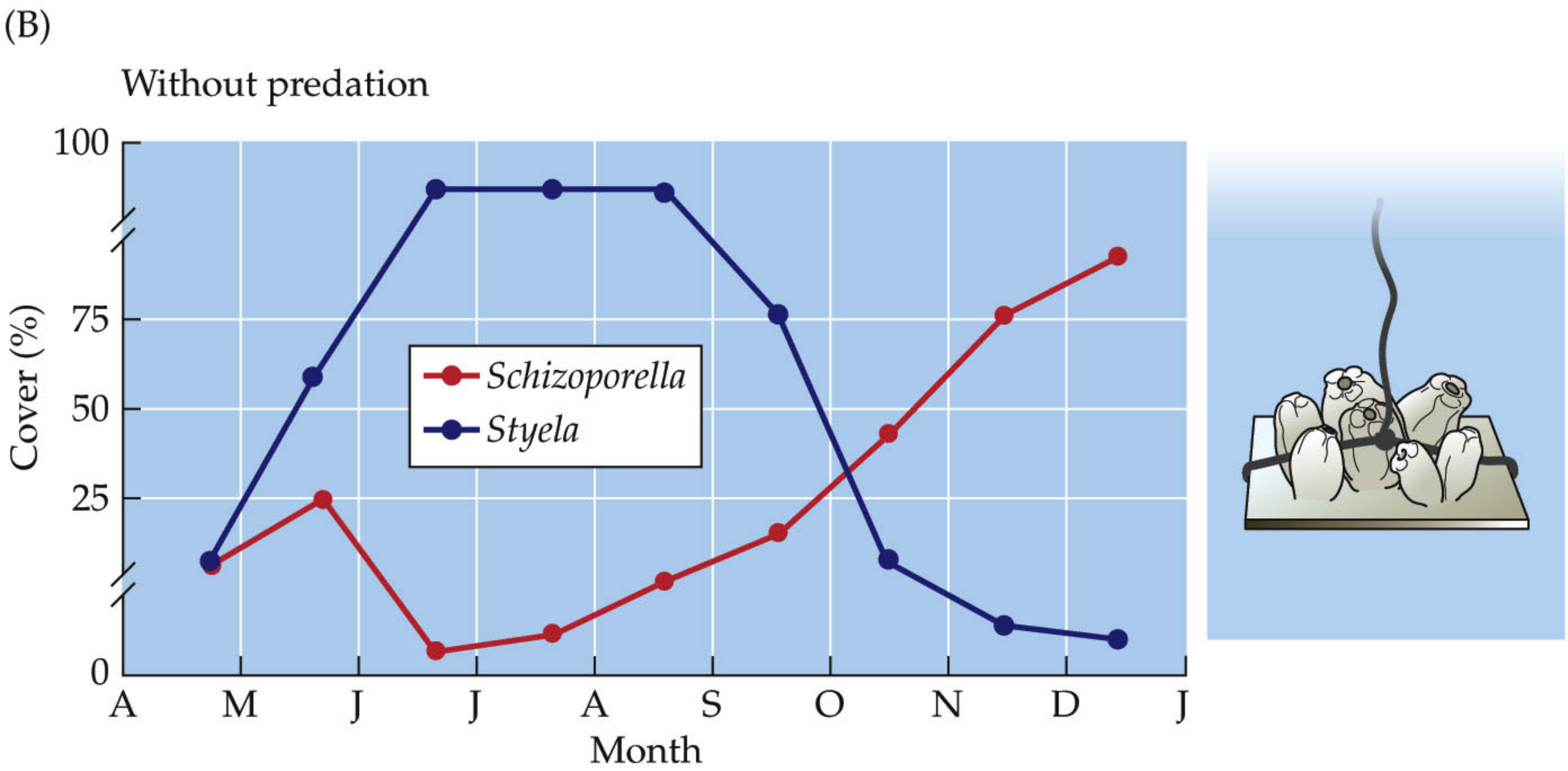
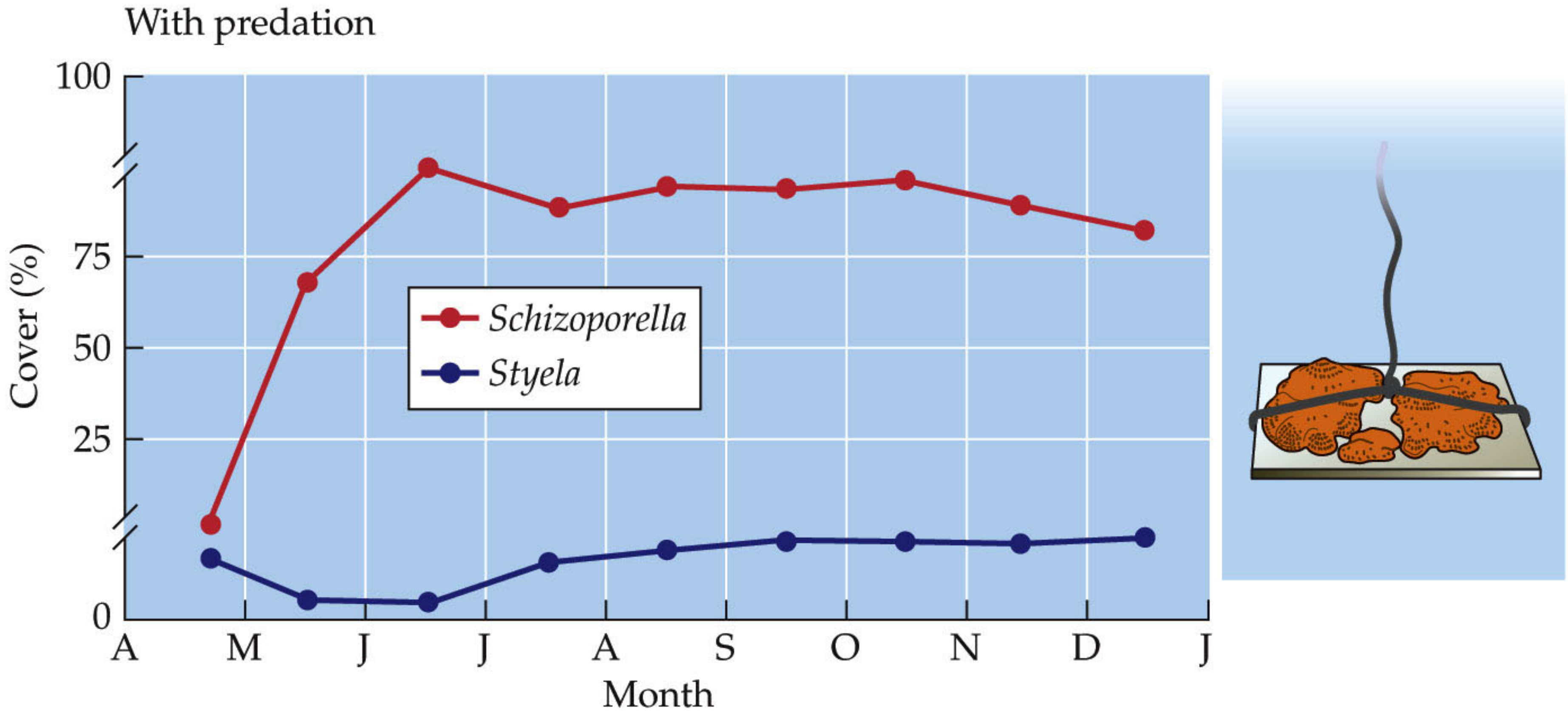


Figure 16.17 Fouling Communities Show Alternative States (Part 3)



Alternative Stable States

Styela also dies off in the winter.

Styela is competitively dominant if left undisturbed, but is outcompeted by *Schizoporella* when disturbed.

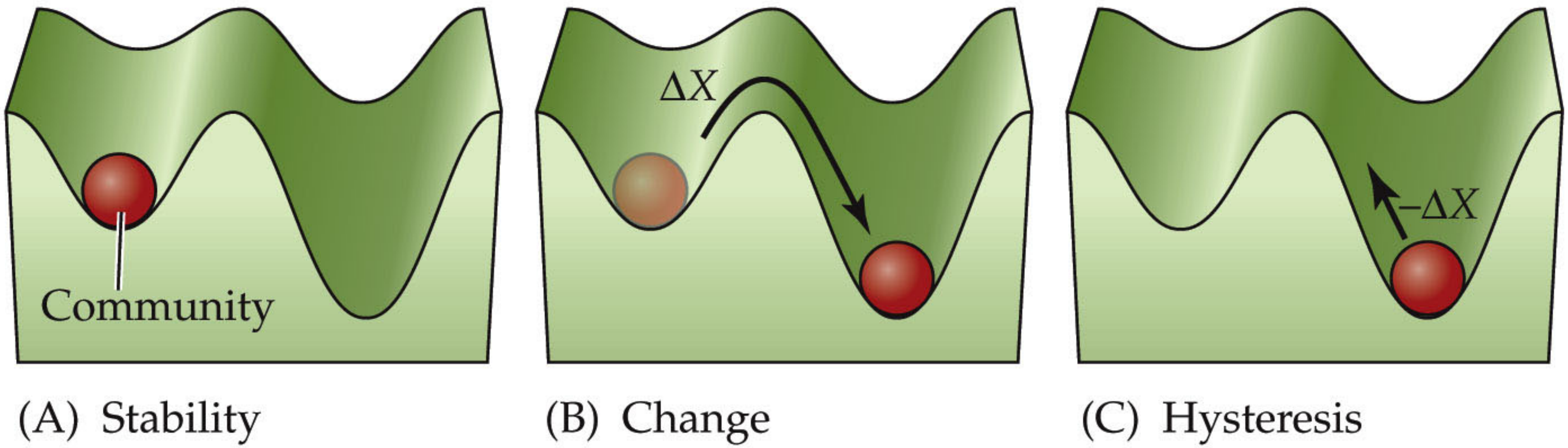
Alternative Stable States

The theory of alternative stable states can be visualized as a topographic surface.

The valleys represent different community types, and a ball represents a community.

The ball can move from one valley to another, depending on presence or absence of strongly interacting species.

Figure 16.18 A Model of Alternative Stable States



Alternative Stable States

A change in one or more dominant species might force the ball into a new valley (stable state).

The ball might not be able to move back into the first valley. **Hysteresis** is an inability to shift back to the original community type, even when original conditions are restored.

Criticism of the tile study included the small spatial scale, and short span of time the experiments were run.

Connell and Sousa (1983) believed that alternative stable states could be driven only by species interactions and not by physical changes in the community.

Their requirement that the physical environment not change is problematic because it excludes as drivers of succession all species that interact with other species by modifying their physical environment—that is, all ecosystem engineers.

This had the effect of delaying research on alternative stable states for 20 years.

Alternative Stable States

Renewed interest has been spurred by evidence that human activities are shifting communities to alternative states.

Examples: Hunting of sea otters, and the effect on sea urchins and kelp forest communities; introduction of the alga *Caulerpa* in the Mediterranean, etc.

Alternative Stable States

The shifts are caused by the removal or addition of key species that maintain a community type.

It is unclear whether the results can be reversed (e.g., “Will the reintroduction of sea otters rejuvenate kelp forests?”).

Case Study Revisited: A Natural Experiment of Mountainous Proportions

In 2000, ecologists revisited Mt. St. Helens to establish a 20-year benchmark of data.

Some had spent all the intervening years studying recolonization and succession in the region.

The result was a book: *Ecological Responses to the 1980 Eruption of Mount St. Helens* (Dale et al. 2005).

Case Study Revisited: A Natural Experiment of Mountainous Proportions

The eruption created disturbances that varied in their effects depending on the distance from the volcano and habitat type.

A surprising number of species survived. Some were still dormant under winter snows. Others were in burrows, or under ice-covered lakes, or were plants with underground parts.

TABLE 16.2

Surviving Organisms Found on Mount St. Helens within a Few Years after the Eruption

Disturbance zone	Mean vegetation cover (%)	Average number of plant species/m^2	Animal species					
			Small mammals	Large mammals	Birds	Lake fish	Amphibians	Reptiles
Pumice Plain	0.0	0.0	0	0	0	0	0	0
Mudflow zone (central flow path)	0.0	0.0	0	0	0	—	0	0
Blowdown zone			8	0	0	4	11	1
Pre-eruption clear-cut	3.8	0.0050						
Forest without snow	0.06	0.0021						
Forest with snow	3.3	0.0064						
Scorch zone	0.4	0.0039		0	0	2	12	1

Source: Adapted from Crisafulli et al. 2005.

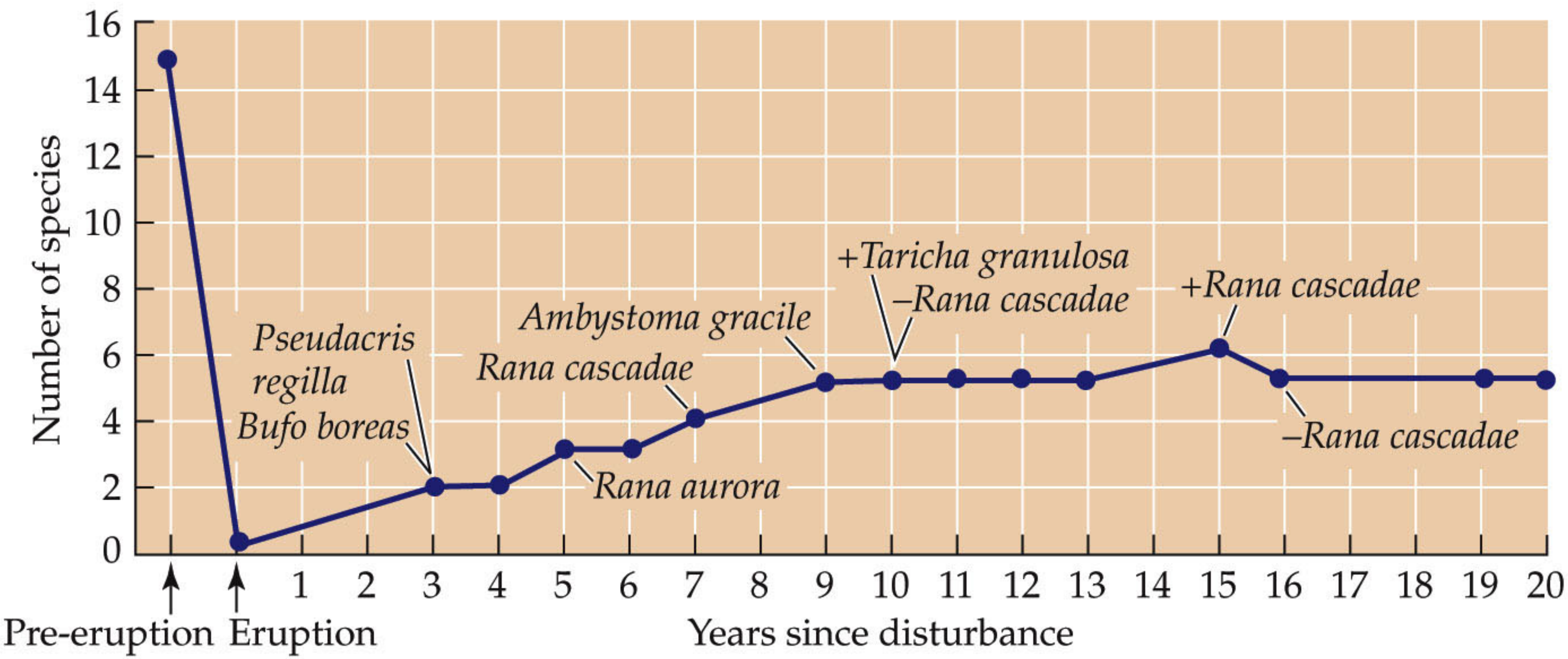
Case Study Revisited: A Natural Experiment of Mountainous Proportions

Survivors have played a role in controlling the pace and pattern of succession.

Some thrived, others didn’t, and there were many surprising outcomes.

Newly-formed and isolated ponds were colonized by amphibians much faster than was thought possible.

Figure 16.19 Rapid Amphibian Colonization



Frogs and salamanders were using tunnels created by northern pocket gophers to make their way from one pond to another.

Case Study Revisited: A Natural Experiment of Mountainous Proportions

Gophers survived in their tunnels. Grassy meadows, their preferred habitat, greatly expanded after the eruption.

Their burrowing activities facilitated plant succession by bringing organic soil, seeds, and fungal spores to the surface.

Figure 16.20 Pocket Gophers to the Rescue

Case Study Revisited: A Natural Experiment of Mountainous Proportions

Multiple mechanisms were responsible for primary succession:

- Facilitation by dwarf lupines—trap seeds and detritus, and have N-fixing bacteria that increases soil N.
- Lupines were inhibited by insect herbivores, which controlled the pace of succession.
- Tolerance—Douglas fir and herbaceous species living together.

All the examples of primary succession have involved plants with N-fixing bacteria.

These bacteria form nodules in the roots of their plant hosts, where they convert N_2 gas from the atmosphere into a form that is usable by plants (NH_4).

The bacteria receive sugars from the plant.

This appears to be extremely important to organisms colonizing barren environments.

Only a few groups of N-fixing bacteria live in plant root nodules—Rhizobia, associated with legumes; and *Frankia*, associated with woody plants such as alders and gale.

Nodule formation is complex.

- Free-living bacteria are attracted to root exudates. They attach to the roots and multiply.

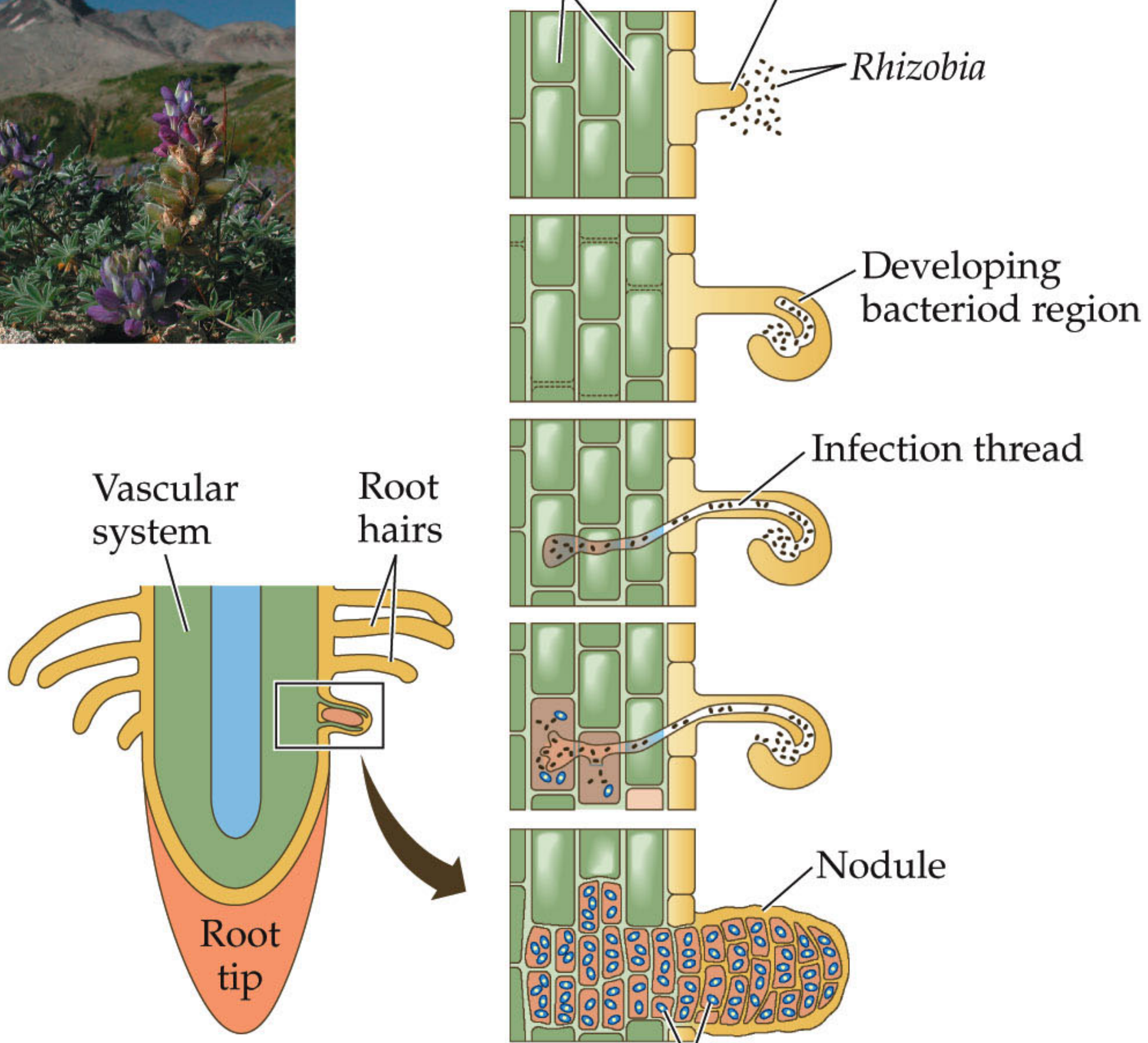
- The bacteria enter the root cells and the cells divide to form a nodule.

- A vascular system develops that supplies sugars to the bacteria and carries fixed nitrogen to the plant.

Figure 16.21 Dwarf Lupines and Nitrogen-fixing Bacteria

(A)

(B)



ECOLOGY, Figure 16.21

Connections in Nature: Primary Succession and Nitrogen-Fixing Bacteria

- The enzymes involved in nitrogen fixing (nitrogenases) are highly sensitive to oxygen and require anaerobic conditions.
- Wherever N-fixing symbioses occur, there is some structural component that produces anaerobic conditions.

- But the bacteria require O_2 for metabolism.

A hemoglobin protein (leghemoglobin) with a very high affinity for O_2 is produced in the nodule to deliver O_2 to the bacteria.

Maintaining the relationship is costly to the plant.

Creating and maintaining the nodules may cost a plant 12%–25% of its total photosynthetic output.

But the benefits include being able to live in environments with few competitors and herbivores.

Connections in Nature: Primary Succession and Nitrogen-Fixing Bacteria

But as they increase the nitrogen content of the soils, they also make conditions better for other species that are likely to be competitors.

Thus their role in early successional environments is extremely important.