# 14

# *Mutualism and Commensalism*

- *Case Study:* The First Farmers
- Positive Interactions
- Characteristics of Mutualism
- Ecological Consequences
- *Case Study Revisited*
- *Connections in Nature*: From Mandibles to Nutrient Cycling

## Case Study: The First Farmers

The fungus-growing ants started cultivating fungi for food at least 50 million years before the first human farmers.

Figure 14.1 Collecting Food for Their Fungi

## Case Study: The First Farmers

The ant farmers nourish, protect, and eat the species they grow, forming a relationship that benefits both the farmer and the crop.

The ants cannot survive without their fungi, many of the fungi cannot survive without the ants.

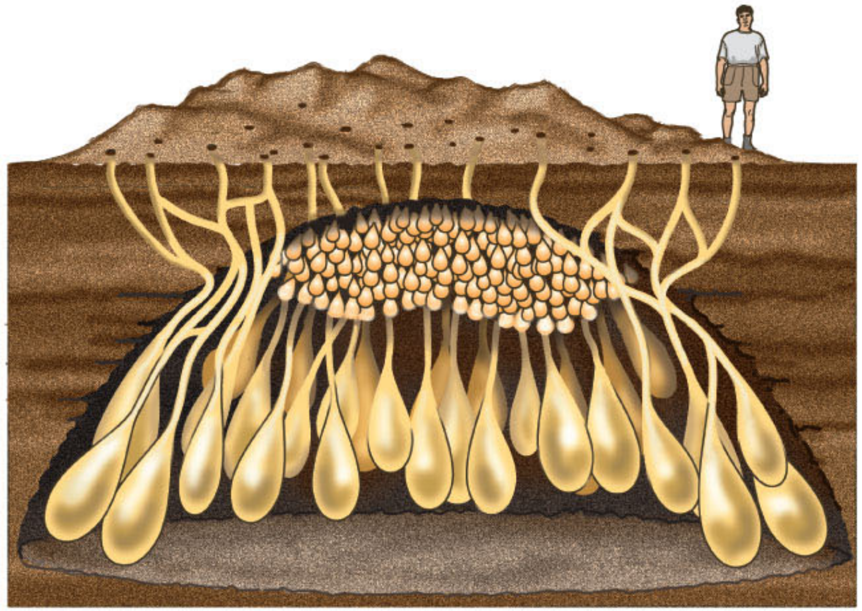
# Case Study: The First Farmers

When a queen leaves the nest to mate and begin a new colony, she carries in her mouth some of the fungi from her birth colony.

The fungi are cultivated in subterranean gardens. A colony may contain hundreds of gardens, each the size of a football; they can provide enough food to support 2–8 million ants.

# Figure 14.2 The Fungal Garden of a Leaf-cutter Ant

(A)



(B)

Leaf-cutter ants cut bits of leaves from plants and feed them to the fungi in their gardens.

*Atta* worker ants maintain trails through the vegetation, and the workers of a single colony can harvest as much plant matter each day as it would take to feed a cow.

## Case Study: The First Farmers

The ants chew the leaves to a pulp, fertilize them with their own droppings, and “weed” the fungal gardens to help control bacterial and fungal invaders.

The fungi produce specialized structures called *gongylidia*, on which the ants feed.

## Case Study: The First Farmers

Both ants and fungi benefit from the relationship.

The ants scrape a waxy covering from the leaves that the fungi have difficulty penetrating.

The fungus digests and renders harmless the chemicals that plants use to kill or deter insect herbivores.

## Case Study: The First Farmers

Nonresident fungi, pathogens, and parasites can sometimes invade the colonies.

What prevents invaders from destroying the gardens?

**Positive interactions** between species are those in which one or both species benefit and neither is harmed.

Example: Most vascular plants form associations with fungi in which the fungus absorbs nutrients from the soil, improving the plant’s growth and survival.

## Introduction

Fossil evidence indicates that the earliest vascular plants formed these associations with fungi more than 400 million years ago (Selosse and Le Tacon 1998).

Early vascular plants lacked true roots, so their interactions with fungi may have aided their colonization of land.

# Positive Interactions

**Concept 14.1: Positive interactions occur when neither species is harmed and the benefits of the interaction are greater than the costs for at least one species.**

**Mutualism**—mutually beneficial interaction between individuals of two species (+/+).

**Commensalism**—individuals of one species benefit, while individuals of the other species do not benefit and are not harmed (+/0).

**Symbiosis**—a relationship in which the two species live in close physiological contact with each other, such as corals and algae.

Parasites can also form symbiotic relationships.

Symbioses can include parasitism (+/–), commensalism (+/0), and mutualism (+/+).

# Positive Interactions

The benefits of positive interactions can take many forms.

Sometimes there is a cost to one or both partners, but the net effect of the interaction is positive because for each species, the benefits are greater than the costs.

Mutualistic associations are everywhere.

Most plants form **mycorrhizae**, symbiotic associations between plant roots and various types of fungi.

The fungi increase the surface area over which the plants can extract soil nutrients (over 3 m of fungal hyphae may extend from 1 cm of plant root).

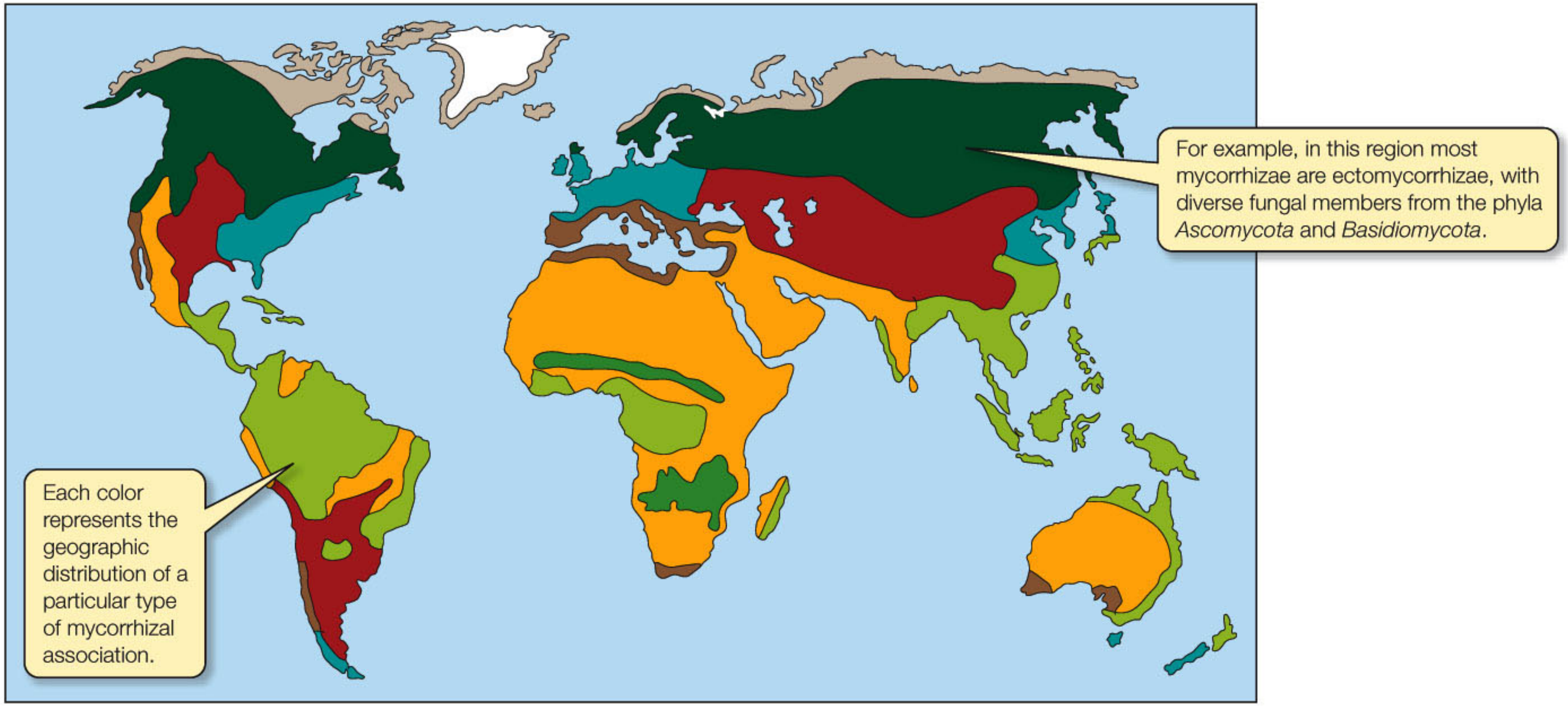
# Positive Interactions

The fungi may also protect the plants from pathogens and help them take up water.

The plants supply the fungi with carbohydrates.

Eight major types of mycorrhizal associations correspond closely with the major terrestrial biomes.

# Figure 14.3 Mycorrhizal Associations Cover Earth's Land Surface



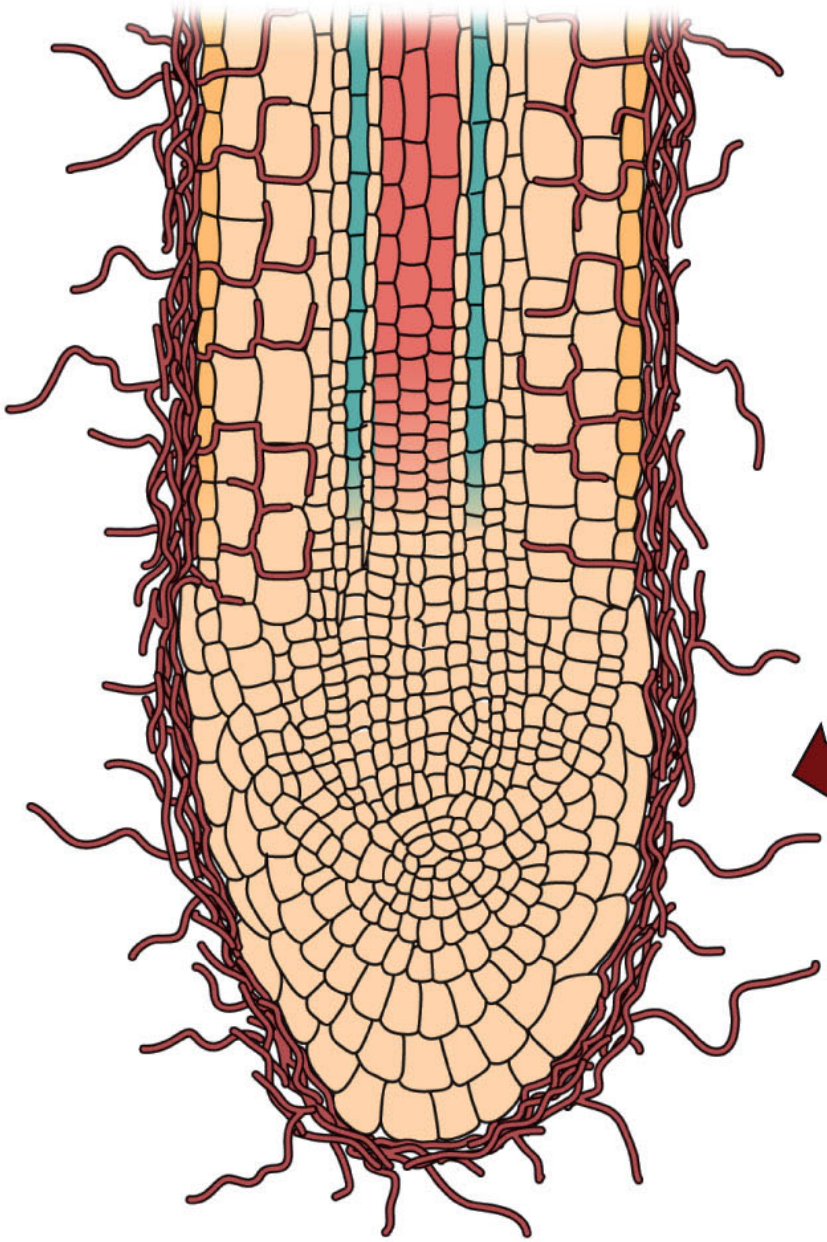
Two categories of mycorrhizae:

**Ectomycorrhizae**—the fungus grows between root cells and forms a mantle around the exterior of the root.

**Arbuscular mycorrhizae**—the fungus grows into the soil, extending some distance away from the root; and also penetrates into some of the plant root cells.

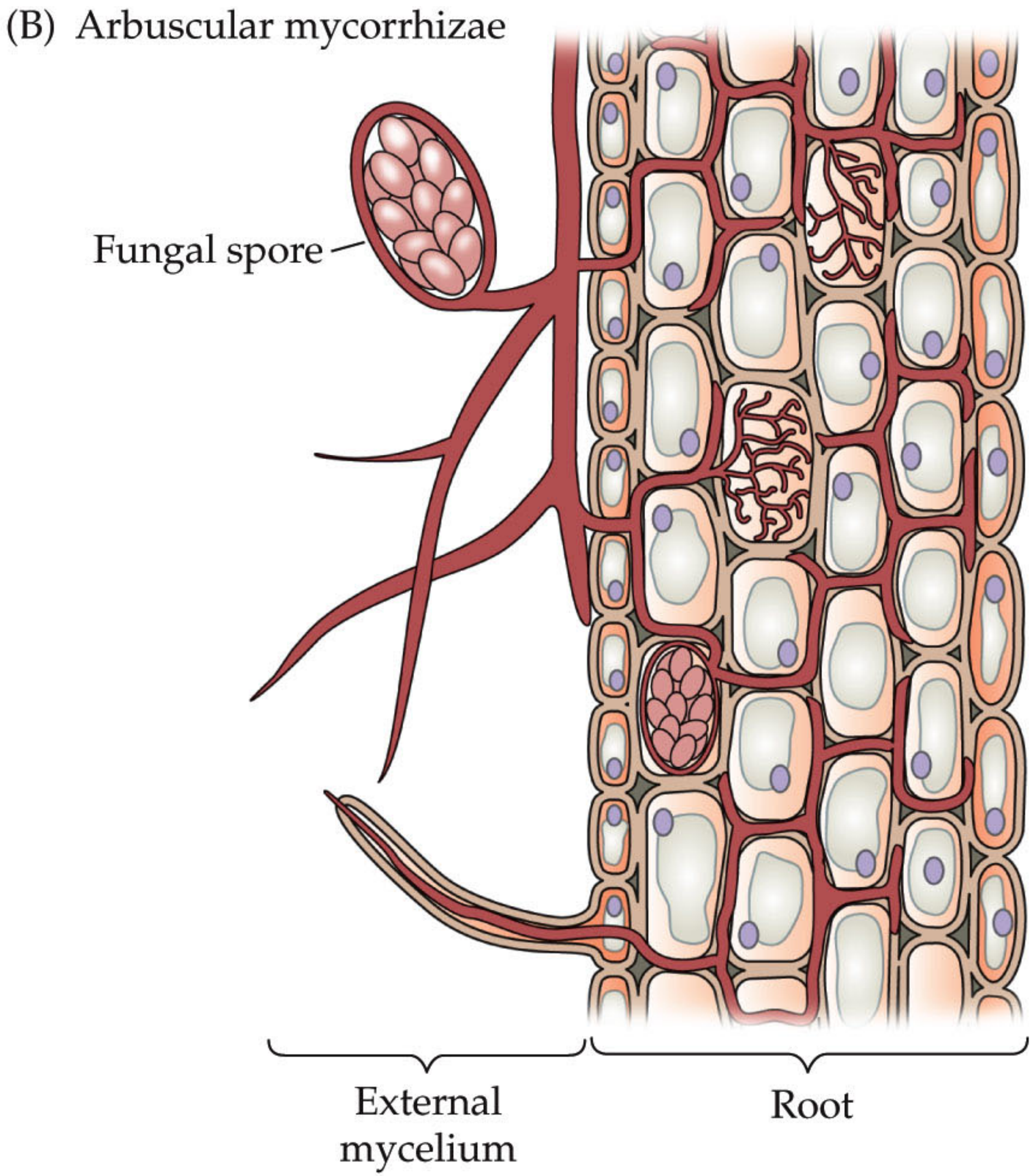
Figure 14.4  Two Major Types of Mycorrhizae (Part 1)

(A) Ectomycorrhizae



ECOLOGY, Figure 14.4 (Part 1)

# Figure 14.4 Two Major Types of Mycorrhizae (Part 2)




**ECOLOGY, Figure 14.4 (Part 2)**

## Positive Interactions

Corals form a mutualism with symbiotic algae.

The coral provides the alga with a home, nutrients (nitrogen and phosphorus), and access to sunlight.

The alga provides the coral with carbohydrates produced by photosynthesis.

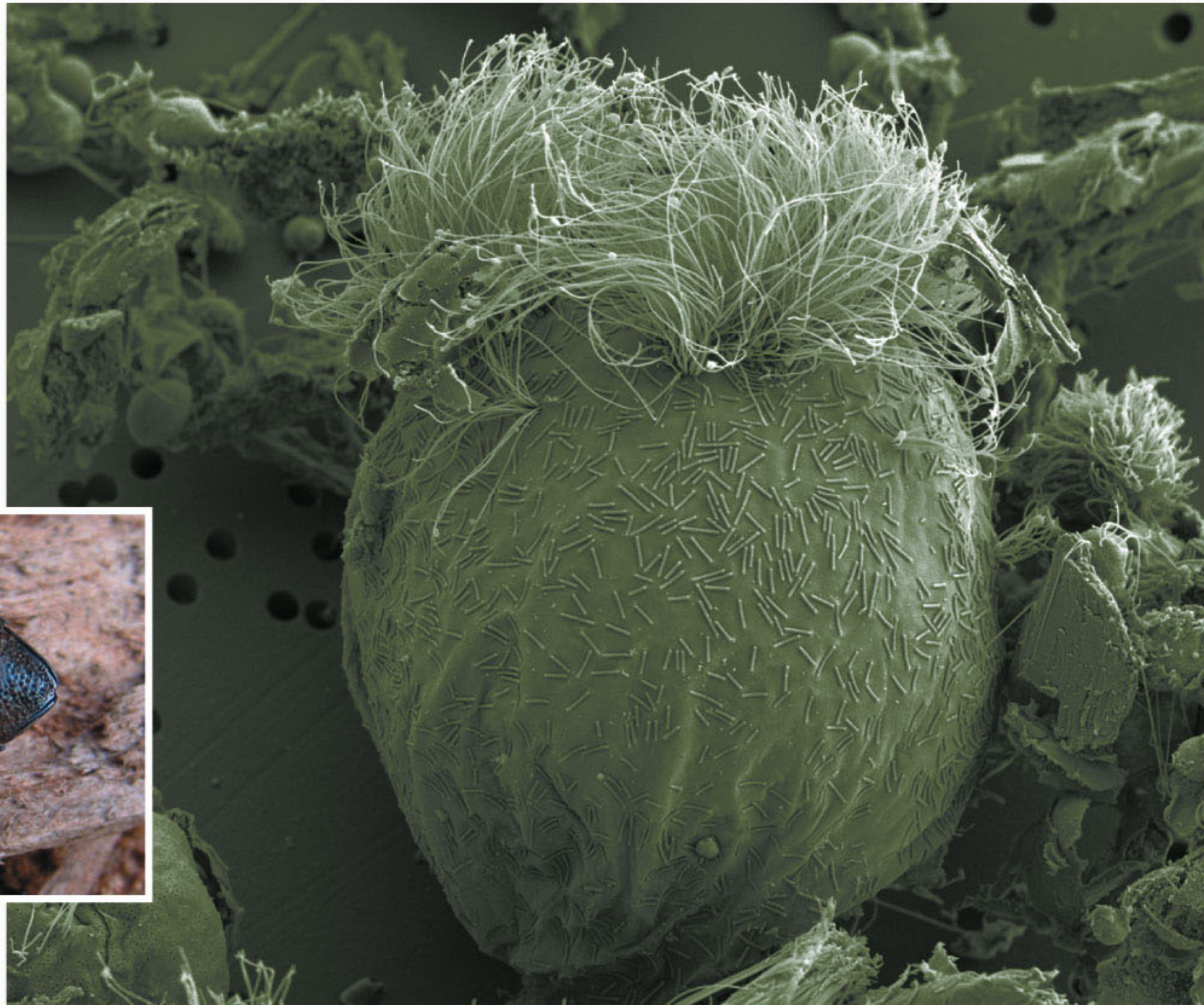
## Positive Interactions

Mammalian herbivores such as cattle and sheep depend on bacteria and protists that live in their guts and help metabolize cellulose.

Insects also have mutualisms with plants, protists, and bacteria. Wood-eating insects have gut protists that can digest cellulose.

# Figure 14.5  A Protist Gut Mutualist

Hypermastigote (*Barbulanympha* sp.)



Wood-eating cockroach (*Cryptocercus punctulatus*)

# Positive Interactions

Commensalism is also everywhere.

Millions of species form +/0 relationships with organisms that provide habitat.

Examples: lichens that grow on trees, bacteria on your skin.

In kelp forests, many species depend on the kelp for habitat, and do no harm to the kelp.

## Positive Interactions

Countless insect and understory plant species live in tropical rainforests and depend on the forests for habitat, yet many have little or no effect on the trees that tower above them.

# Positive Interactions

Different types of ecological interactions can evolve into commensalism or mutualism.

Example: Lichens on tree leaves may initially harm the tree by blocking sunlight. The Australian palm has adapted by increasing the concentration of chlorophyll in parts of leaves that are covered with lichens.

Mutualism can arise from a host–parasite interaction.

This was observed in a strain of *Amoeba proteus* that was infected by a bacterium.

Initially, the bacteria caused the hosts to be smaller, grow slowly, and often killed the hosts.

But parasites and hosts can coevolve.

Five years later, the bacterium had evolved to be harmless to the amoeba; the amoeba had evolved to be dependent on the bacterium for metabolic functions.

Various tests showed that the two species could no longer exist alone (Jeon 1972).

# Positive Interactions

Some positive interactions are highly species-specific, and obligate (not optional for either species).

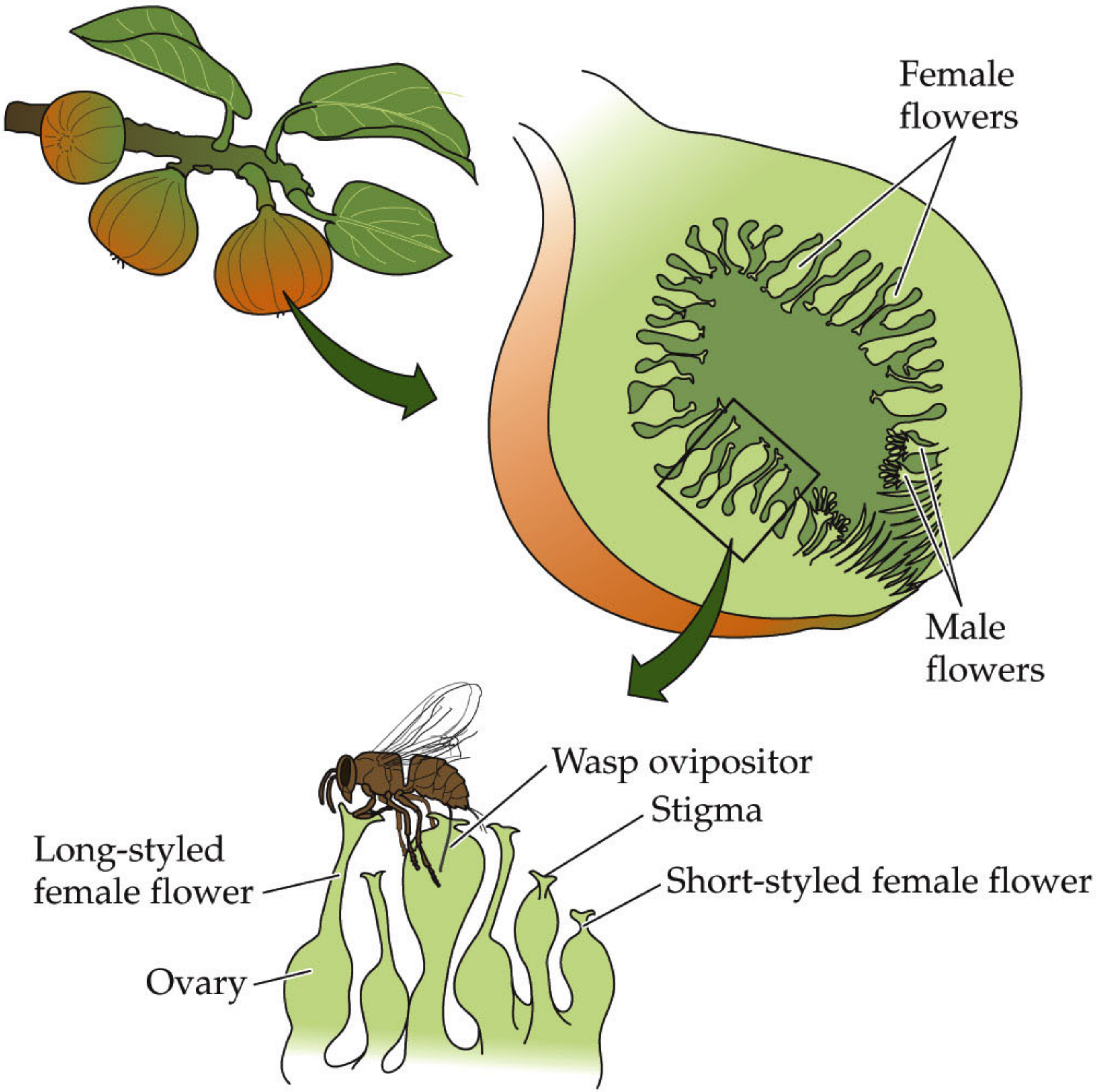
Example: The leaf cutter ants and fungus cannot survive without each other, and the interaction has led both to evolve unique features that benefit the other species.

# Positive Interactions

Tropical figs are pollinated by one or a few species of fig wasps. Neither species can reproduce without the other.

The wasps and the figs have coevolved. The wasps have complex reproductive behaviors in the fig receptacle that ensures that the fig flowers get pollinated, and the next generation of wasps are hatched.

# Figure 14.6 Fig Flowers and the Wasp That Pollinates Them




**ECOLOGY, Figure 14.6**

# Positive Interactions

Many mutualisms and commensalisms are facultative (not obligate) and show few signs of coevolution.

In deserts, the shade of adult plants creates cooler, moister conditions. Seeds of many plants can only germinate in this shade.  The adult is called a **nurse plant**.

## Positive Interactions

One species of nurse plant may protect the seedlings of many other species.

Desert ironwood serves as a nurse plant for 165 different species.

The nurse plant and the beneficiary species may evolve little in response to one another.

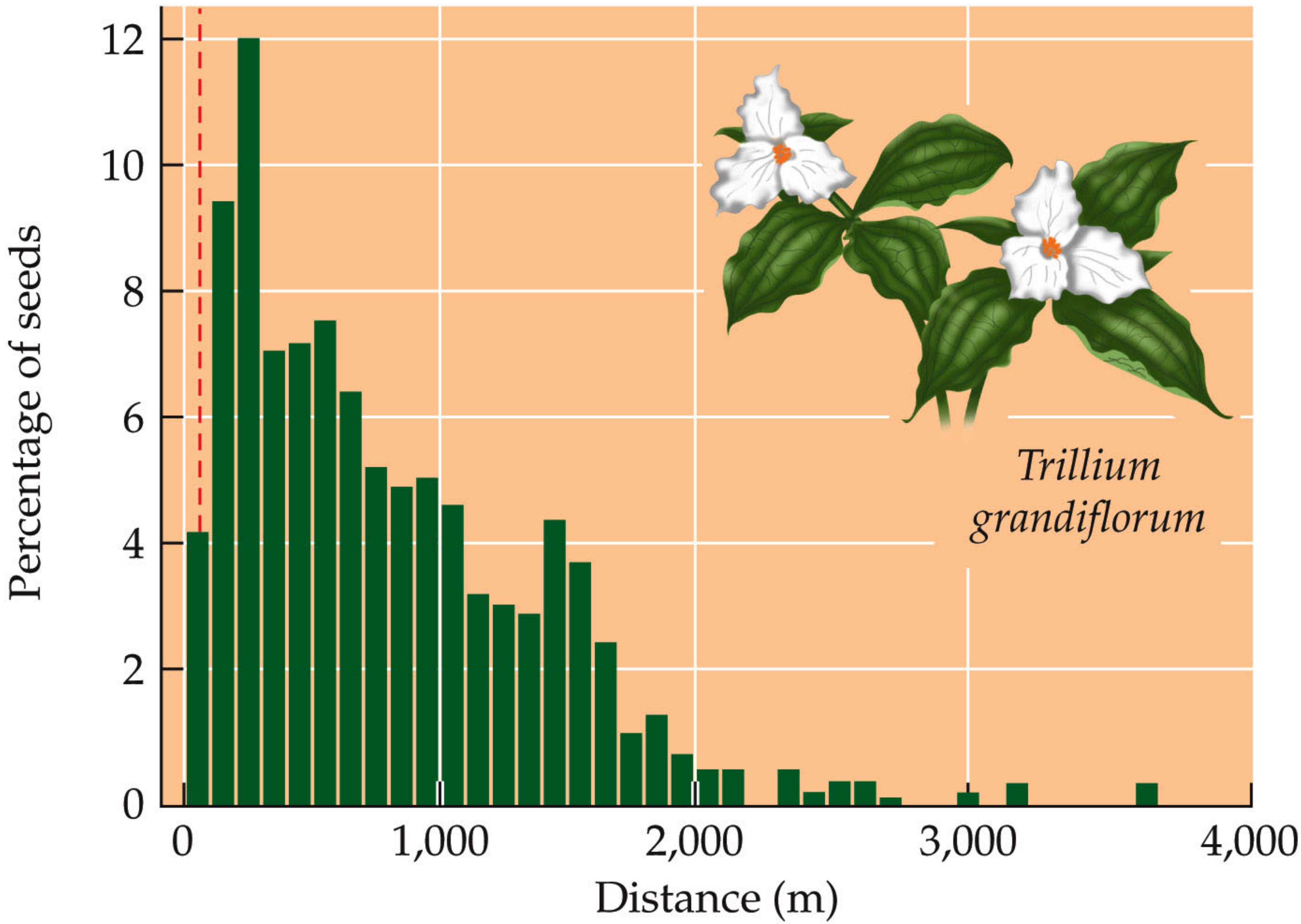
## Positive Interactions

Large herbivores such as deer or moose often consume seeds of herbaceous plants.

Many of the seed pass through unharmed, and are deposited with the feces. Thus, it becomes a dispersal mechanism.

Such interactions are sporadic and facultative; there is little evidence to suggest that the species have coevolved.

# Figure 14.7 Deer Can Move Plant Seeds Long Distances




**ECOLOGY, Figure 14.7**

## Positive Interactions

Interactions between two species can be categorized by the outcome for each species:

- Positive (benefits > costs)
- Negative (costs > benefits)
- Neutral (benefits = costs)

But costs and benefits can vary in time and space.

# Positive Interactions

Soil temperature can determine whether a pair of wetland plants are commensals or competitors.

Wetland soils can be anoxic. Some plants such as cattails can aerate soils by passively transporting oxygen through continuous air spaces in their leaves, stems, and roots.

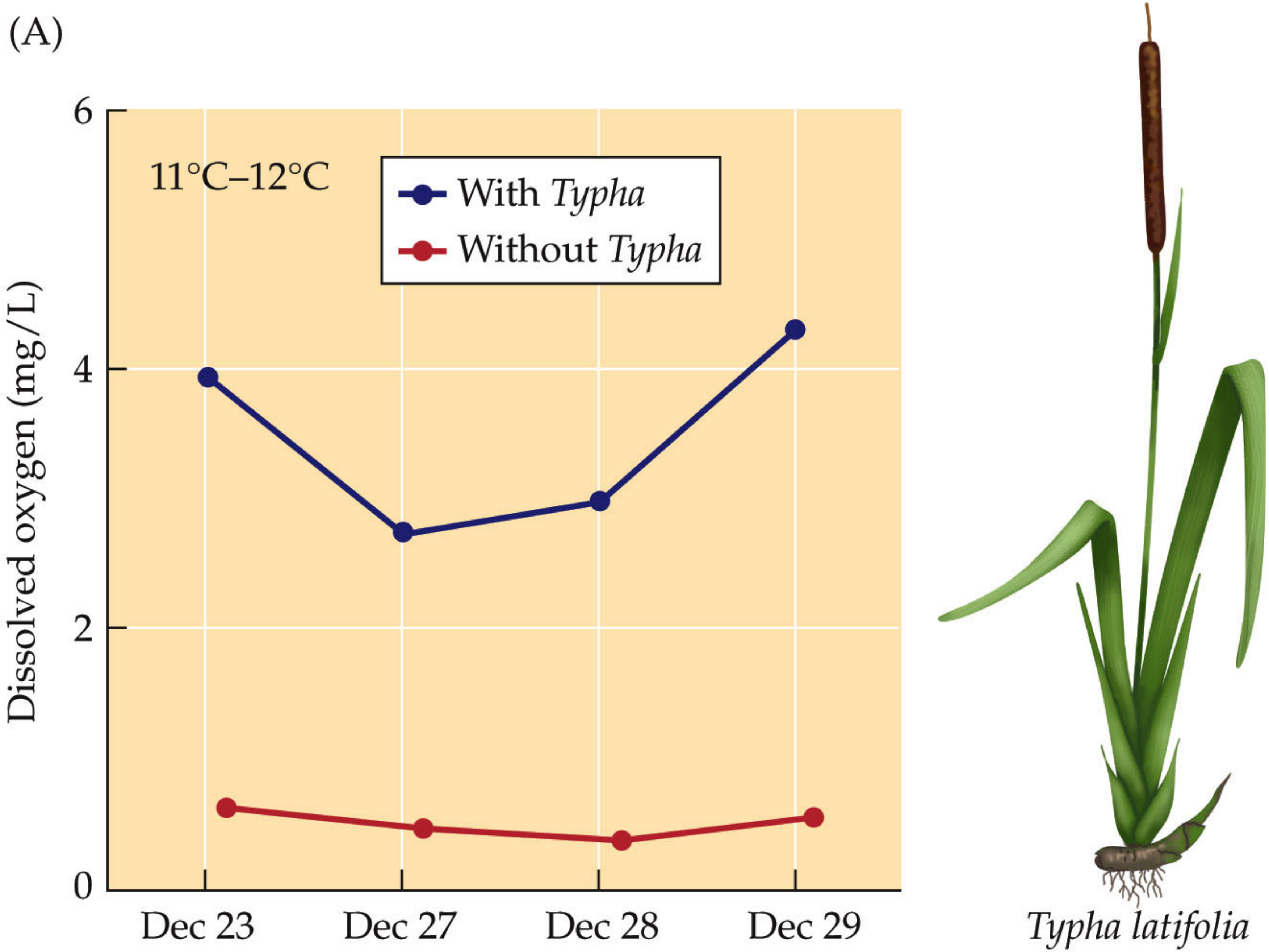
Some of this oxygen becomes available to other plants.

An experiment with cattails (*Typha latifolia*) and *Myosotis laxa* (small-flowered forget-me-not, a species that lacks continuous air spaces):

The plants were grown at two different temperatures.

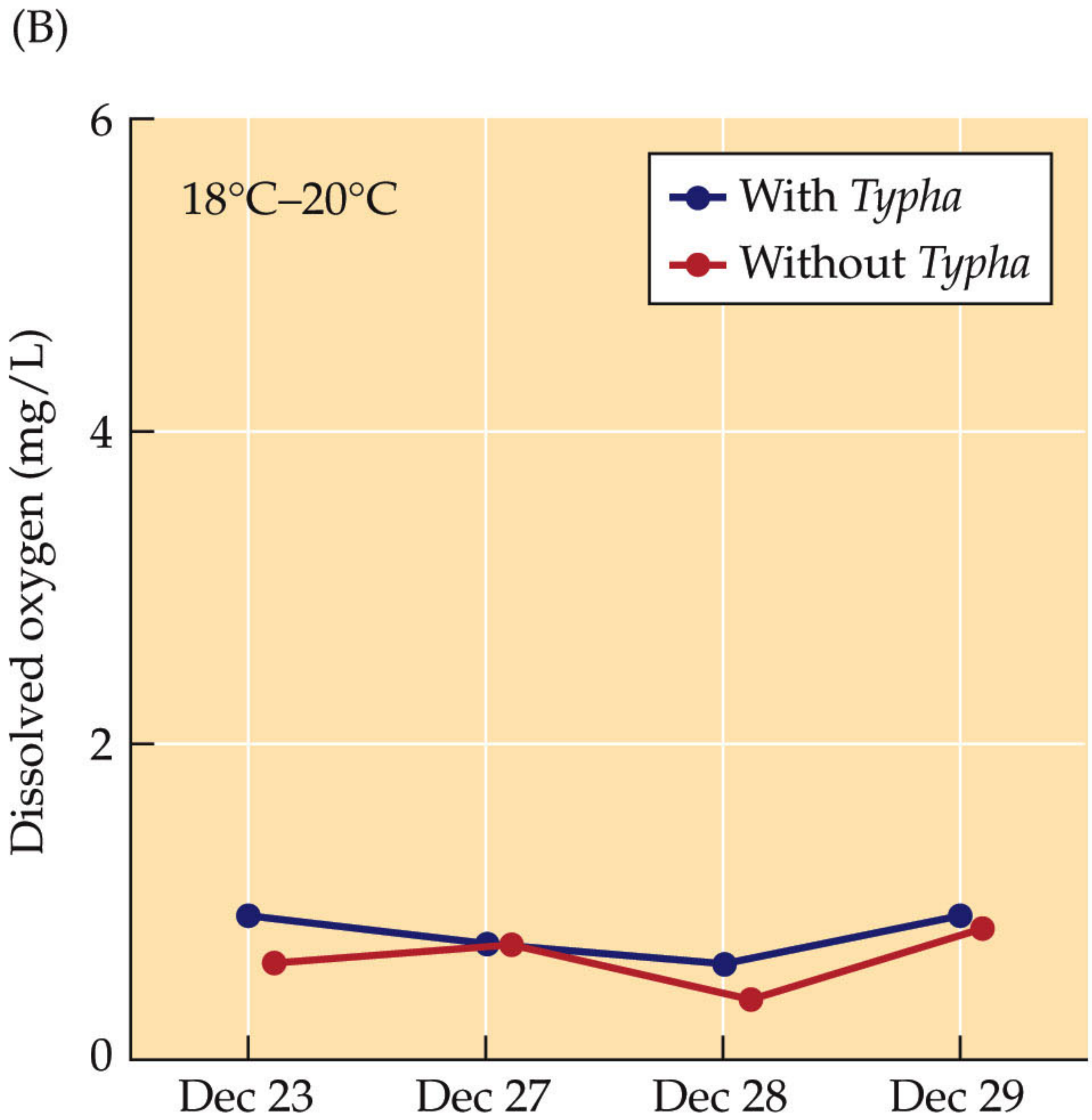
At low temperatures, soil oxygen increased when *Typha* was present, but not at the higher temperature.

Figure 14.8 A Wetland Plant Aerates the Soil under Some Conditions (Part 1)




ECOLOGY, Figure 14.8 (Part 1)

Figure 14.8 A Wetland Plant Aerates the Soil under Some Conditions (Part 2)



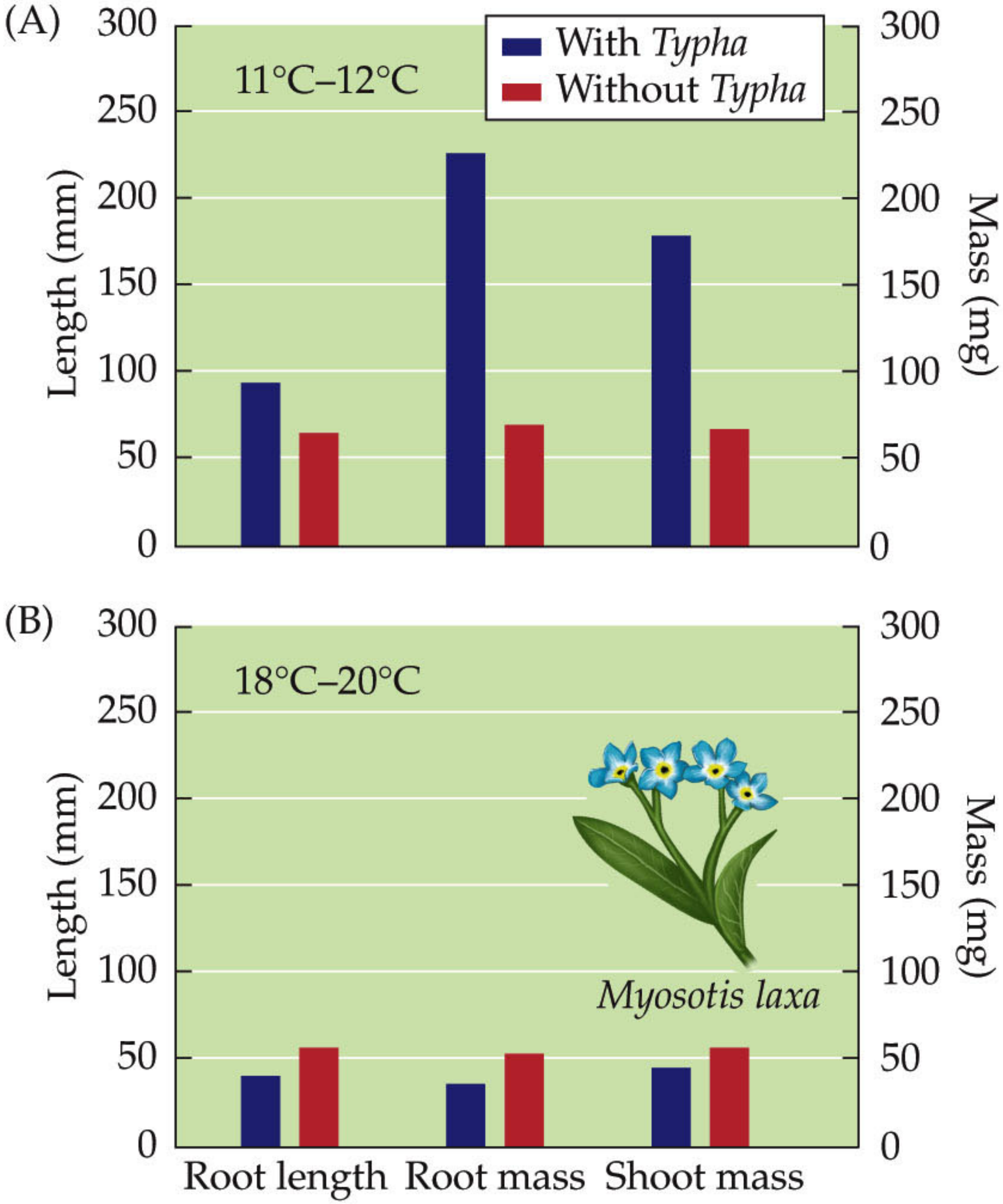
## Positive Interactions

At low temperatures, growth of *Myosotis* increased when *Typha* was present.

At the higher temperature, the presence of *Typha* decreased growth of *Myosotis*.

At low temperatures *Typha* had a positive effect on *Myosotis*, but a negative effect at high temperatures.

# Figure 14.9 From Benefactor to Competitor




**ECOLOGY, Figure 14.9**

# Positive Interactions

Many recent studies have shown that positive interactions are important in many communities.

Studies often compare performance of a target species when neighbors are present with its performance when neighbors are removed.

# Positive Interactions

An international groups of ecologists looked at the effects of neighboring plants on 115 target species.

Performance was measured as change in biomass or leaf number.

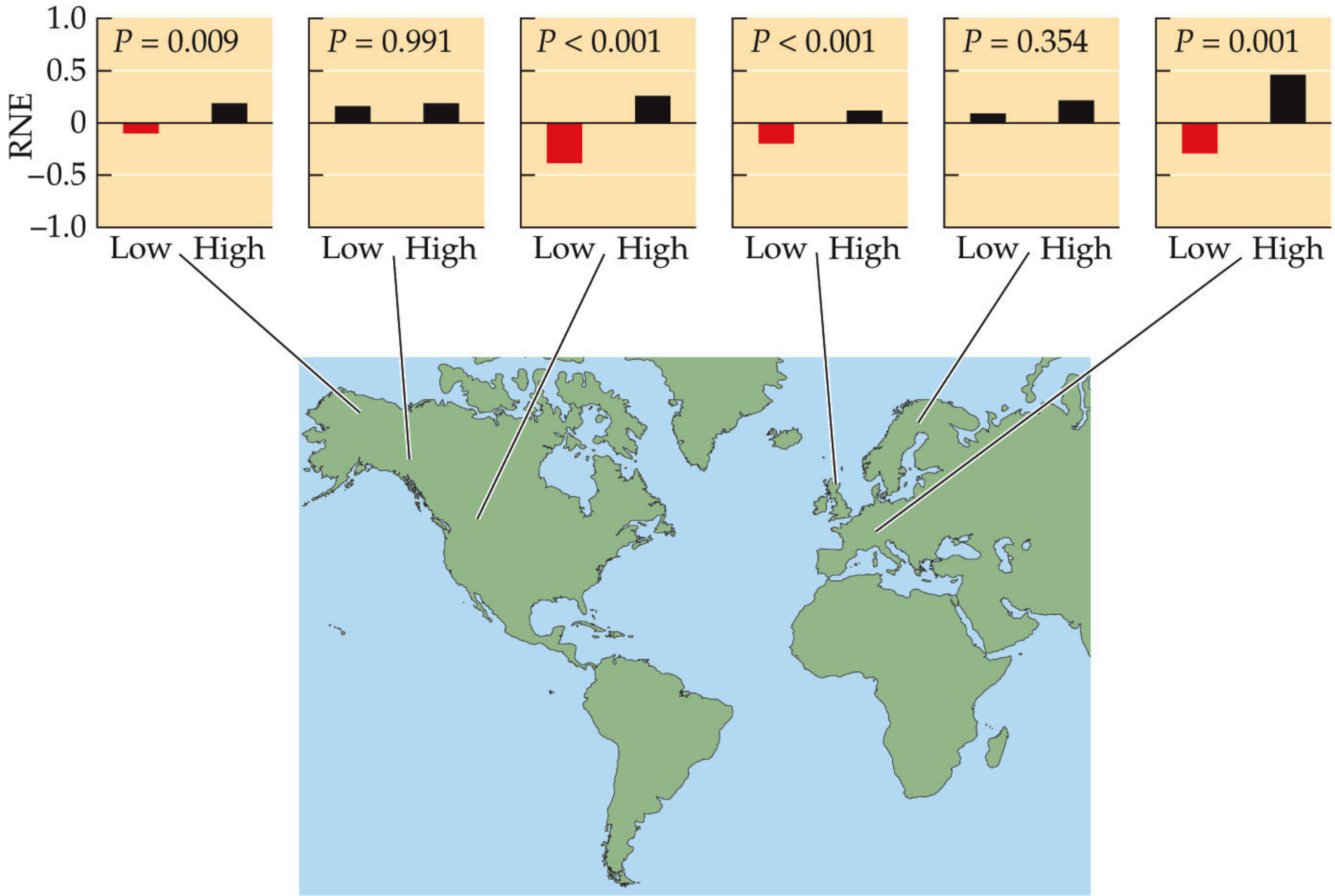
The “relative neighbor effect” (RNE) = target species’ performance with neighbors present minus its performance when neighbors were removed.

## Positive Interactions

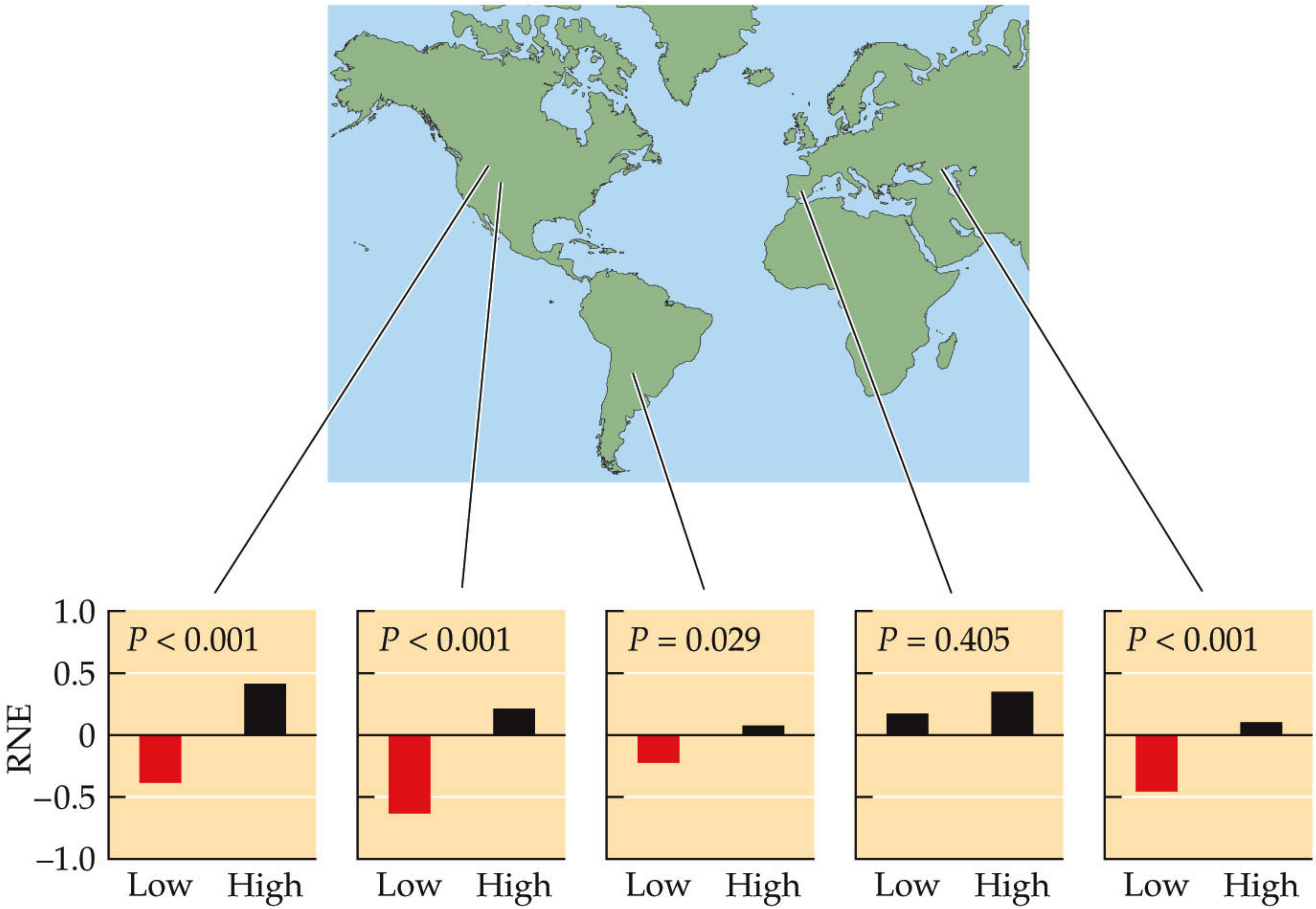
RNE was generally positive at high-elevation sites, indicating that neighbors had a positive effect on the target species.

RNE was generally negative at low-elevation sites.

# Figure 14.10 Neighbors Increase Plant Performance at High-Elevation Sites (Part 1)



# Figure 14.10 Neighbors Increase Plant Performance at High-Elevation Sites (Part 2)



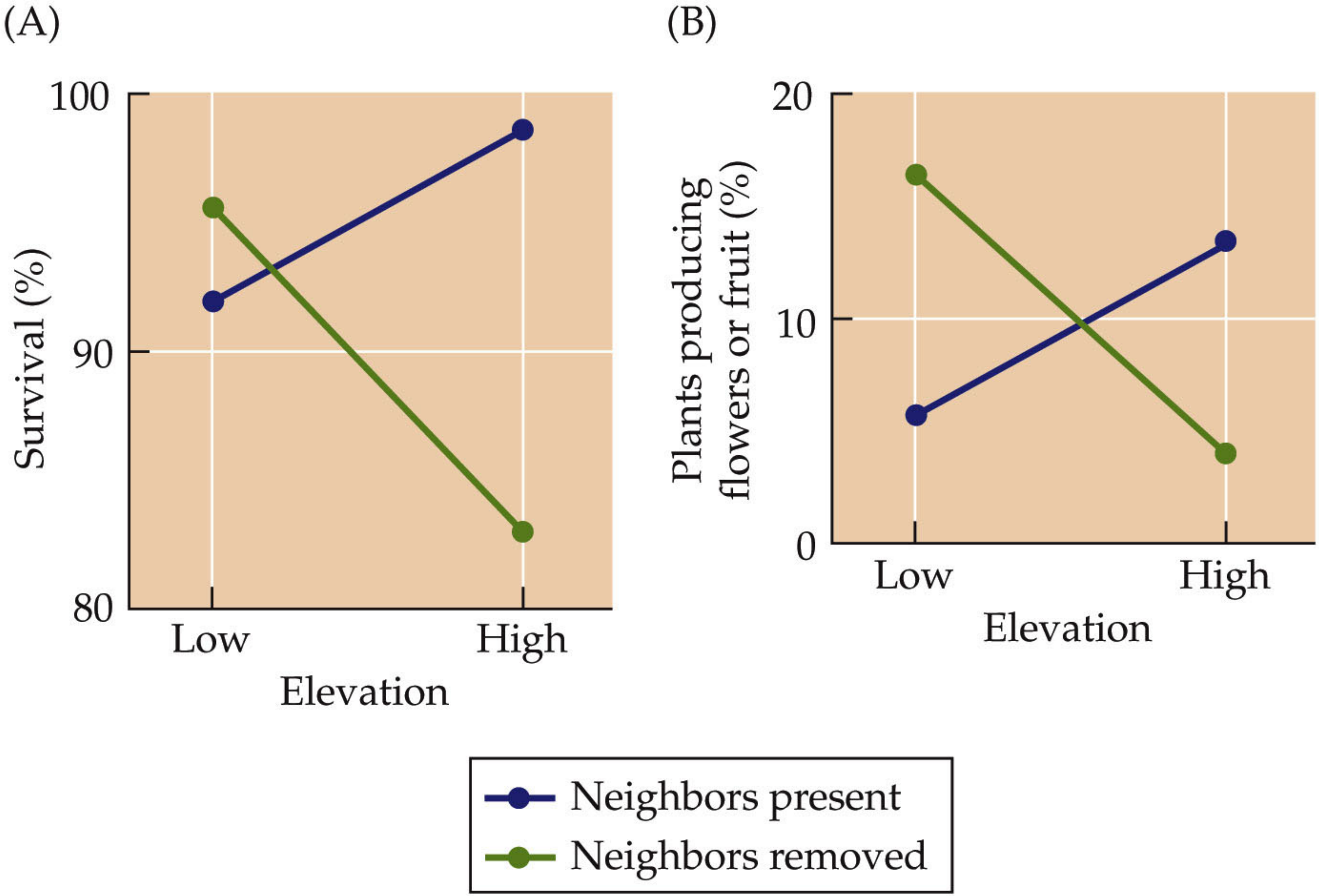

**ECOLOGY, Figure 14.10 (Part 2)**

## Positive Interactions

At high-elevation sites, neighbors also tended to increase the target species survival and reproduction.

Neighbors had the opposite effect at low-elevation sites.

## Figure 14.11 Negative Effects at Low Elevations, Benefits at High Elevations



## Positive Interactions

Because environmental conditions tend to be more extreme at high-elevation sites, these results suggest that positive interactions may be more common in stressful environments.

Similar results have been found in intertidal communities.

## Characteristics of Mutualism

**Concept 14.2: Each partner in a mutualism acts to serve its own ecological and evolutionary interests.**

Mutualisms can be categorized by the type of benefits that result.

Often, the two partners may receive different types of benefits, and the mutualism can be classified two ways.

## Characteristics of Mutualism

**Trophic mutualisms**—a mutualist receives energy or nutrients from its partner.

Example: Leaf-cutter ants and fungus.

In mycorrhizae, the fungus gets energy in the form of carbohydrates and the plant gets help in taking up limiting nutrients, such as phosphorus.

**Habitat mutualisms**—one partner provides the other with shelter, a place to live, or favorable habitat.

Example: Alpheid (pistol) shrimp dig a burrows that that they share with a goby fish. The goby gets a refuge, and in turn serves as a “seeing eye fish” for the nearly blind shrimp.

# Figure 14.12 A Seeing-Eye Fish

The grass *Dichanthelium lanuginosum* grows next to hot springs in soils whose temperatures can be as high as 60°C.

It has a fungal symbiont that grows throughout the plant.

Experiments showed that grass plants without their symbiont could not survive at 60°C.

# Characteristics of Mutualism

In field experiments, grass plants with symbionts had greater root and leaf mass than plants without symbionts in soil temperatures up to 40°C.

In soils above 40°C, plants with symbionts continued to grow well, but all grass plants without symbionts died.

## Characteristics of Mutualism

In another study, the symbiont was transferred to watermelons, tomatoes, and wheat.

These plants were then able to survive high temperature soils.

## Characteristics of Mutualism

**Service mutualisms**—interactions in which one partner performs an ecological service for the other.

Ecological services include pollination, dispersal, and defense against herbivores, predators, or parasites.

## Characteristics of Mutualism

Although both partners in a mutualism benefit, there are also costs.

In the coral–alga mutualism, the cost to the coral includes supplying nutrients and space; the cost to the alga is giving up some of the carbohydrates it could use for itself.

# Characteristics of Mutualism

Sometimes the cost is clear—a “reward” for a service.

During flowering, milkweeds use up to 37% of the energy gain from photosynthesis to produce nectar that attracts insect pollinators.

# Characteristics of Mutualism

In a mutualism, the net benefits must exceed the net costs for both partners.

If environmental conditions change and benefit is reduced or cost increased for either partner, the outcome of the interaction may change, particularly for facultative interactions.

## Characteristics of Mutualism

Some ants protect treehoppers from predators, and the treehoppers secrete "honeydew" (sugar solution), which the ants feed on.

Treehoppers always secrete honeydew, so ants always have this resource.

But when predators are few, the tree-hoppers may get no benefit from the ants. The interaction may shift from +/+ to +/0.

## Figure 14.13 A Green Weaver Ant Guards Its Treehopper Mutualist

## Characteristics of Mutualism

A mutualist may withdraw the reward that it usually provides.

In high-nutrient environments, plants can easily get nutrients, and may reduce the carbohydrate reward to mycorrhizal fungi.

The costs of supporting the fungus are greater than the benefits the fungus can provide.

## Characteristics of Mutualism

**Cheaters** are individuals that increase offspring production by overexploiting their mutualistic partner.

If this happens, the interaction probably won’t persist.

Several factors contribute to the persistence of mutualisms.

# Characteristics of Mutualism

"Penalties" may be imposed on cheaters.

Pellmyr and Huth (1994) documented this in an obligate, coevolved mutualism between a yucca and its exclusive pollinator, the yucca moth.

The female moth collects pollen with specialized mouthparts. She lays eggs in another yucca, and then deliberately deposits the pollen in this flower.

# Figure 14.14 Yuccas and Yucca Moths

(A) (B)

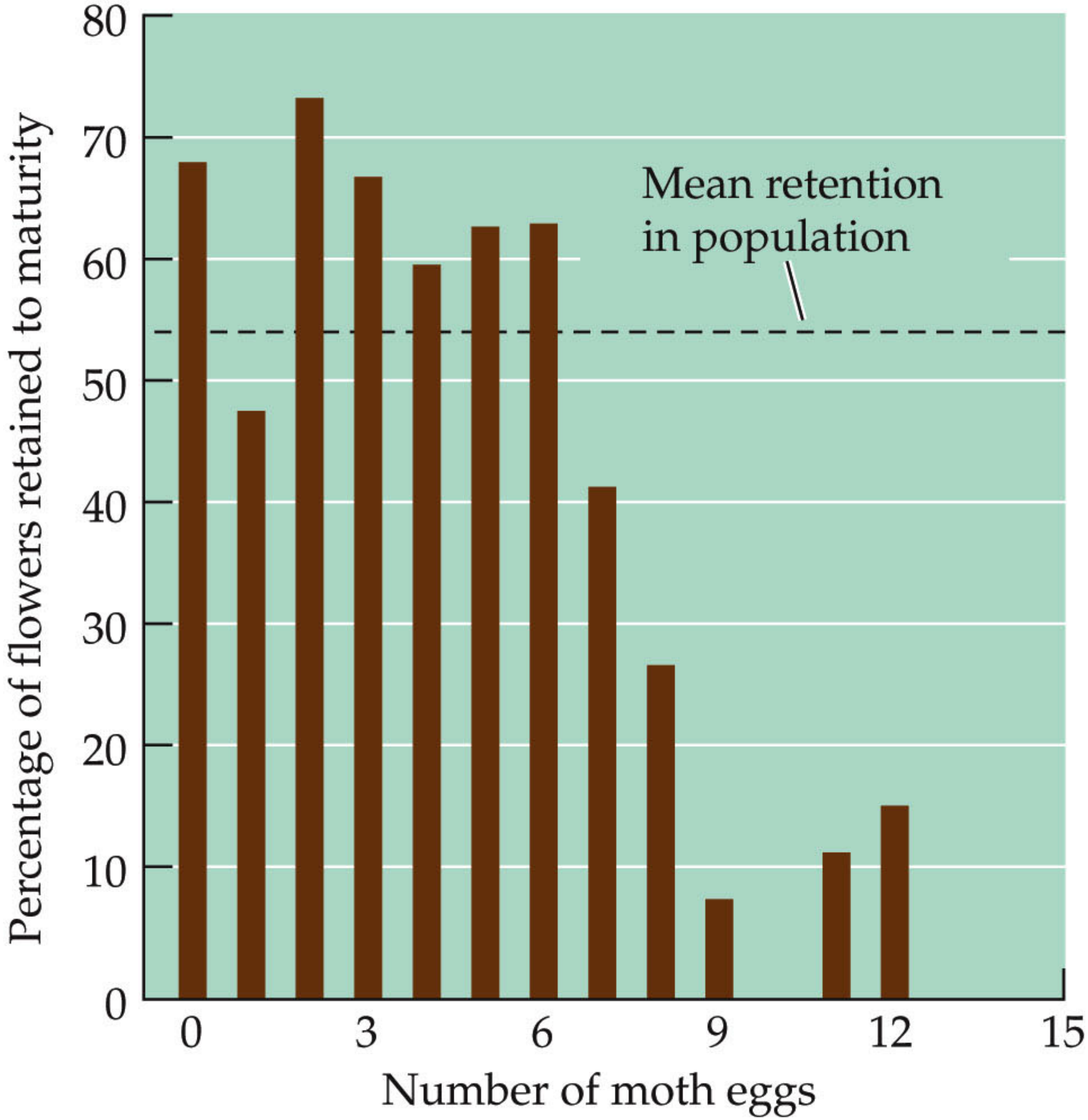
# Characteristics of Mutualism

The larvae complete development by eating the seeds in the flower.

Exploitation can occur if moths lay too many eggs and hence consume too many seeds.

Yuccas are able to abort flowers with too many eggs, before the moth larvae hatch.

## Figure 14.15 A Penalty for Cheating




*ECOLOGY*, **Figure 14.15**

## Characteristics of Mutualism

The partners in a mutualism are not altruistic.

Both partners take actions that promote their own best interests.

In general, a mutualism evolves and is maintained because the net effect is advantageous to both partners.

**Concept 14.3: Positive interactions affect the distributions and abundances of organisms as well as the composition of ecological communities.**

Mutualism can influence demographic factors.

This is demonstrated by ants (*Pseudomyrmex*) and acacia trees.

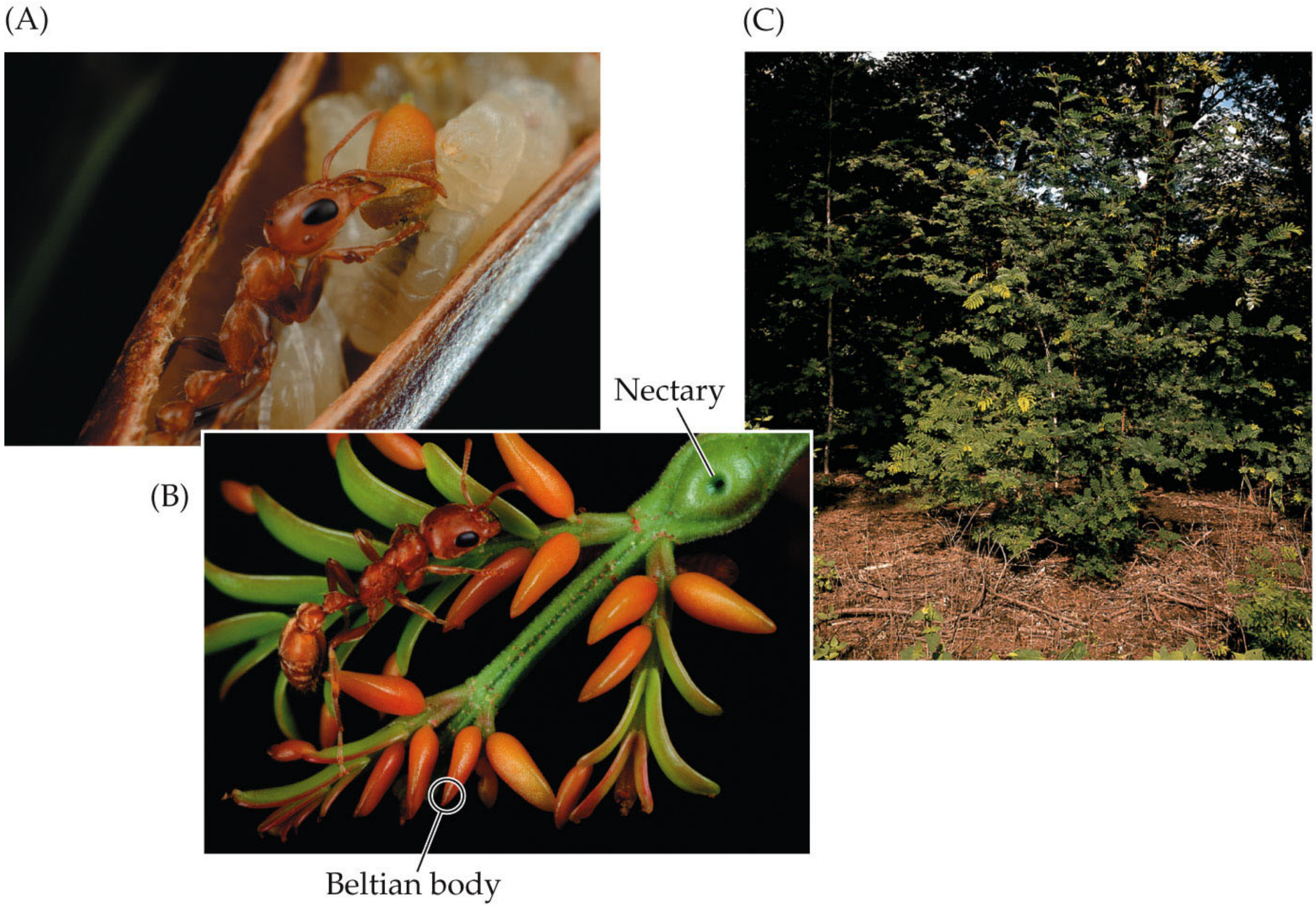
## Ecological Consequences

The trees have large thorns, which house ant colonies.

The tree produces Beltian bodies on the leaf tips, which are high in protein and fat. The ants gather these to feed to the larvae.

Ant workers patrol the tree 24 hours a day and aggressively attack insect and even mammal herbivores.

# Figure 14.16 An Ant–Plant Mutualism



## Ecological Consequences

The ants also use their mandibles to maul other plants within 10–150 cm the tree, providing the acacia with a competitor-free zone.

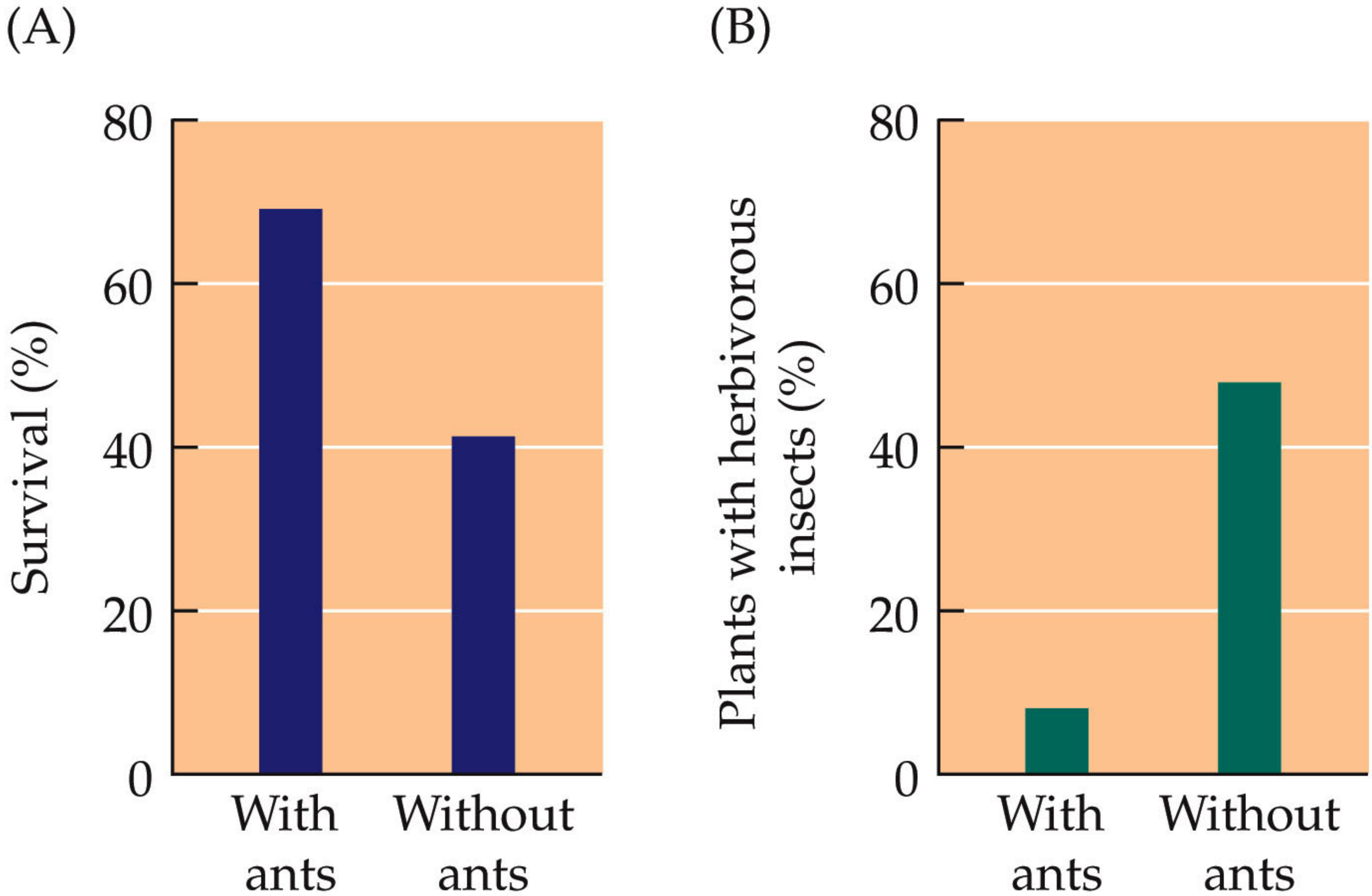
## Ecological Consequences

To determine the benefits the acacias receive, Janzen (1966) removed ants from some and compared them to trees with their ants.

Acacias with ant colonies weighed over 14 times as much as plants without ant colonies.

They also survived better and were attacked by insect herbivores less frequently.

## Figure 14.17 Effects of a Mutualism with Ants on Swollenthorn Acacias




*ECOLOGY*, Figure 14.17

# Ecological Consequences

Acacias without ant colonies are often killed by herbivores in 6–12 months.

The ants also cannot survive without the trees.

Both species have evolved unusual characteristics that benefit the other species.

# Ecological Consequences

The ants are highly aggressive, attacking both herbivores and other plants. Other ants in this genus don’t have this trait.

The acacias have enlarged thorns, specialized nectaries, and Beltian bodies, and produce leaves nearly year-round (providing a reliable food source for the ants).

# Ecological Consequences

When one species provides another with favorable habitat, it influences the distribution of that species.

Examples: Corals and algal symbionts; the grass *Dichanthelium* and its fungal symbiont.

# Ecological Consequences

It is very common for a group of dominant species (such as trees in a forest) to determine the distributions of other species by physically providing the habitat on which they depend.

Many plant and animal species are found only in forests; they can’t tolerate conditions (or competitors) in other habitats.

## Ecological Consequences

In rocky intertidal zones, many species live under the strands of seaweed that grow on the rocks. The seaweed creates a moist, cool environment at low tide.

Beach grasses stabilize the sand and enable the formation of entire communities of plants and animals.

## Ecological Consequences

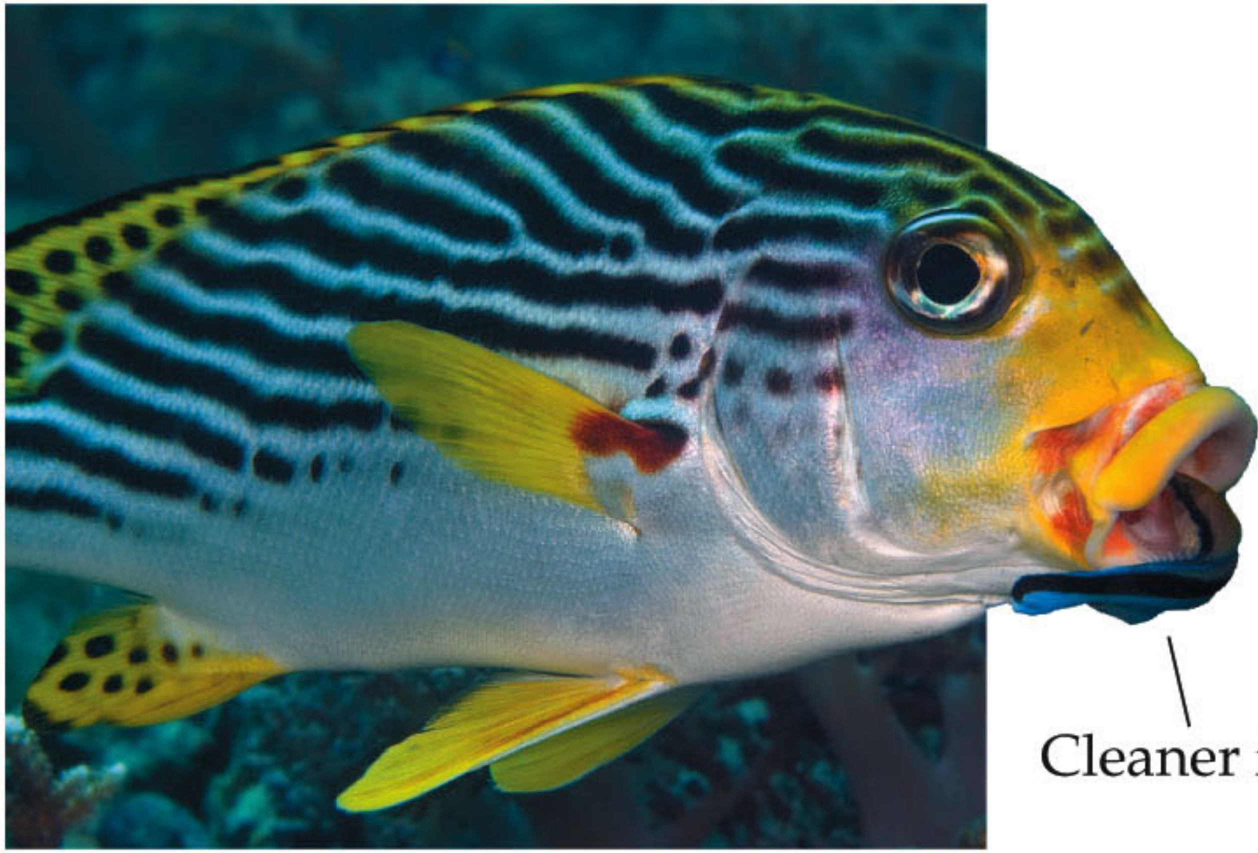
Positive interactions can also influence community composition and ecosystem properties.

Many coral reef fish have service mutualisms with smaller organisms (cleaners) that remove parasites from the fish (clients).

The benefit the client receives is greater than the energy benefit it could gain by eating the cleaner.

Figure 14.18 A  Ecological effects of the cleaner fish, *Labroides dimidiatus*

(A)



## Ecological Consequences

Studies of a cleaner fish on the Great Barrier Reef showed that individuals were visited by an average of 2,297 clients each day, from which the cleaner fish removed (and ate) an average of 1,218 parasites per day.

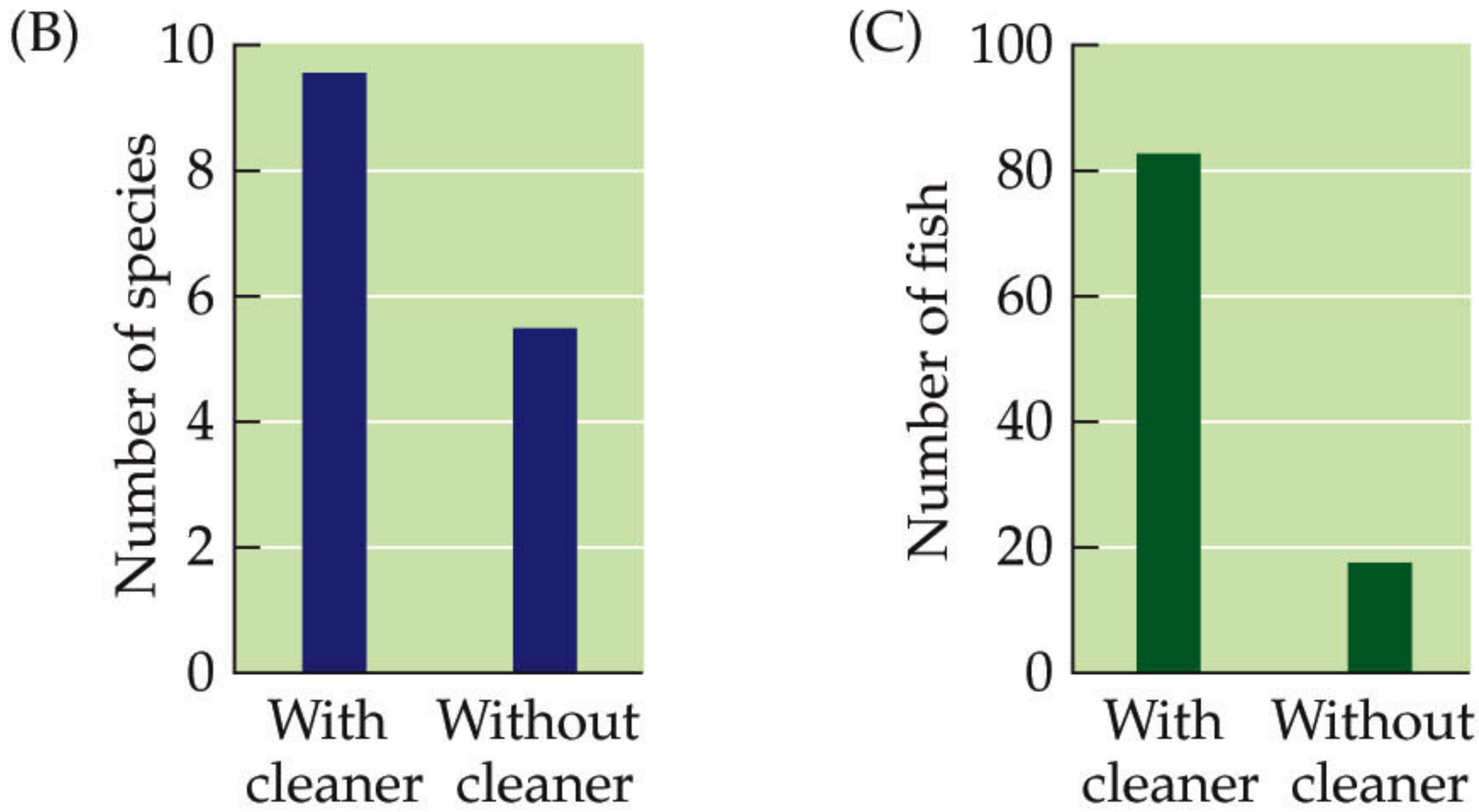
# Ecological Consequences

In an experiment, the cleaner fish were removed from five small reefs.

After 12 days, there were 3.8 times more parasites on one fish species than in control reefs.

After 18 months, the abundance and number of fish species on the reefs had decreased.

## Figure 14.18 B,C Ecological effects of the cleaner fish, *Labroides dimidiatus*



## Ecological Consequences

In an experiment with two prairie grasses, Hetrick et al. (1989) grew them in a greenhouse with and without mycorrhizal fungi.

When mycorrhizal fungi were present, big bluestem grass dominated; when absent, junegrass dominated.

# Ecological Consequences

In a natural prairie, Hartnett and Wilson (1999) suppressed mycorrhizal fungi with a fungicide.

Big bluestem (which had been dominant) decreased, while a variety of other species increased.

The mycorrhizal fungi may have given big bluestem a competitive advantage.

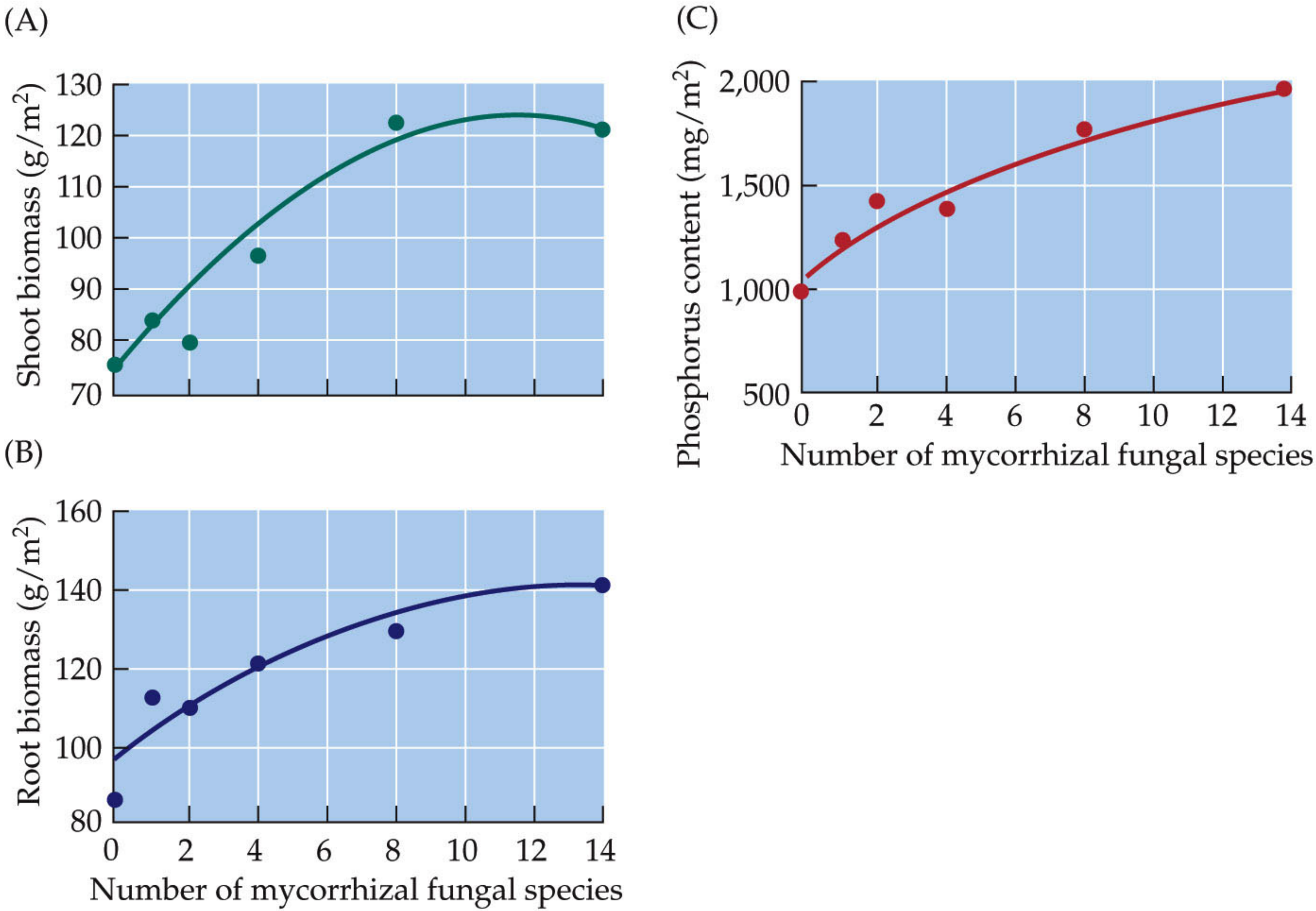
# Ecological Consequences

In a large-scale field experiment, the species of mycorrhizal fungi were manipulated.

Soils with different numbers of fungal species were seeded with 15 plant species.

In one growing season, plant root and shoot biomass, and phosphorus uptake increased as the number of fungal species increased.

# Figure 14.19 Mycorrhizal Fungi Affect Ecosystem Properties




**ECOLOGY, Figure 14.19**

# Ecological Consequences

Thus, mutualistic interactions can influence key features of ecosystems, such as net primary productivity and the supply and cycling of nutrients such as phosphorus.

## Case Study Revisited: The First Farmers

In 1999, a parasitic fungus (*Escovopsis*) was discovered that attacks the fungal gardens of leaf-cutter ants.

The parasite can be transmitted from one garden to another, and rapidly destroy the gardens, leading to death of the ant colony.

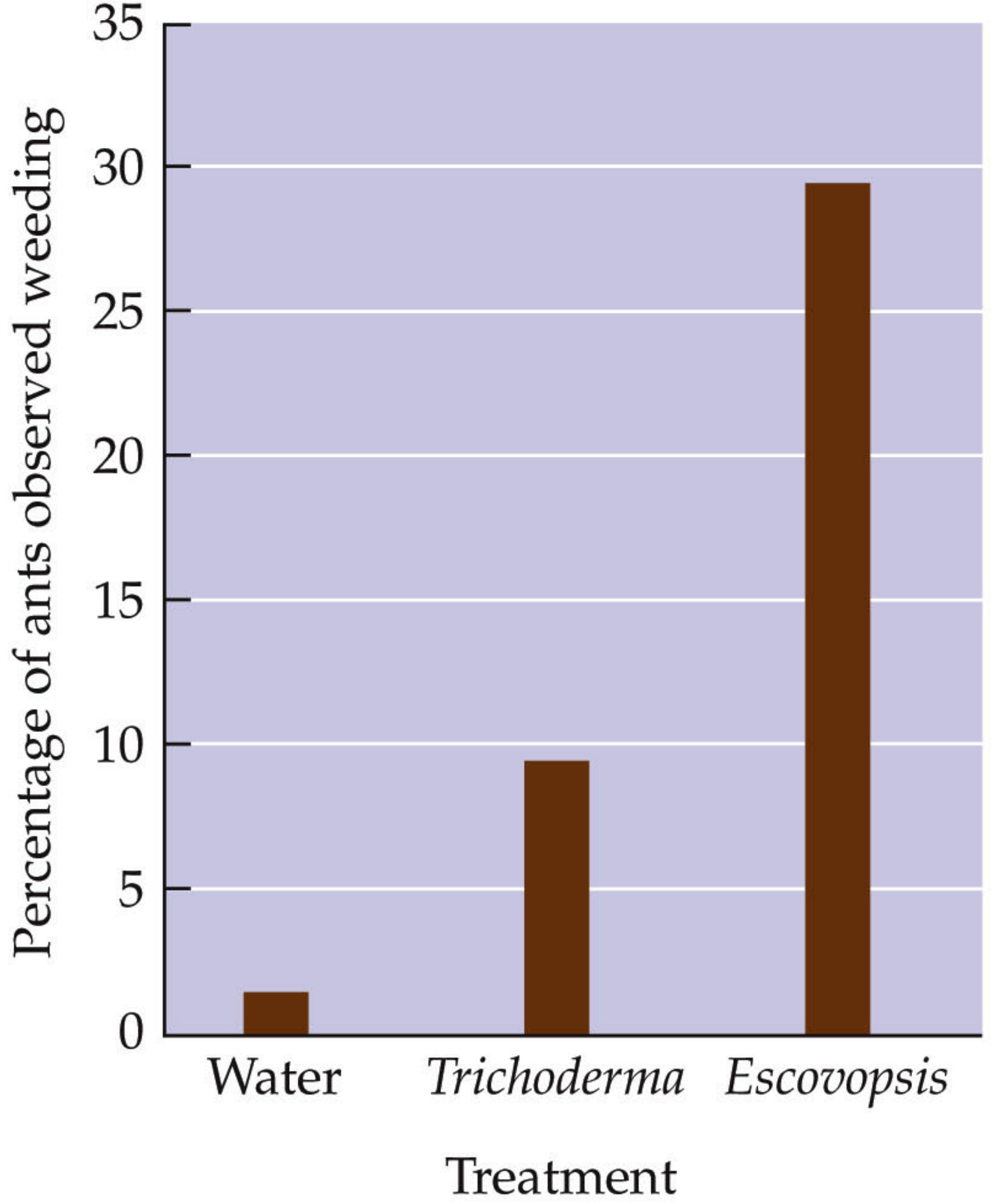
## Case Study Revisited: The First Farmers

Ants respond to *Escovopsis* by increasing the garden weeding rate.

They also appear to enlist the help of other species. The ants carry a bacterium that makes chemicals that inhibit *Escovopsis*.

The bacteria also secrete compounds that promote the growth of the cultivated fungi.

# Figure 14.20 A Specialized Parasite Stimulates Weeding by Ants



The bacteria also benefit: They get a place to live (in specialized structures called crypts on the ant's exoskeleton and a source of food (glandular secretions) from the ants.

Thus, the bacterium is a third mutualist.

## Case Study Revisited: The First Farmers

The ant colonies cultivate a single clone of the fungus.

This fungus actively rejects fungi introduced from outside the colony.

The more different the invading fungus is genetically, the stronger the rejection.

The fungus thus imposes single-crop farming on the leaf-cutter ants.

# Figure 14.21 Resident Fungi Inhibit Foreign Fungi (Part 1)

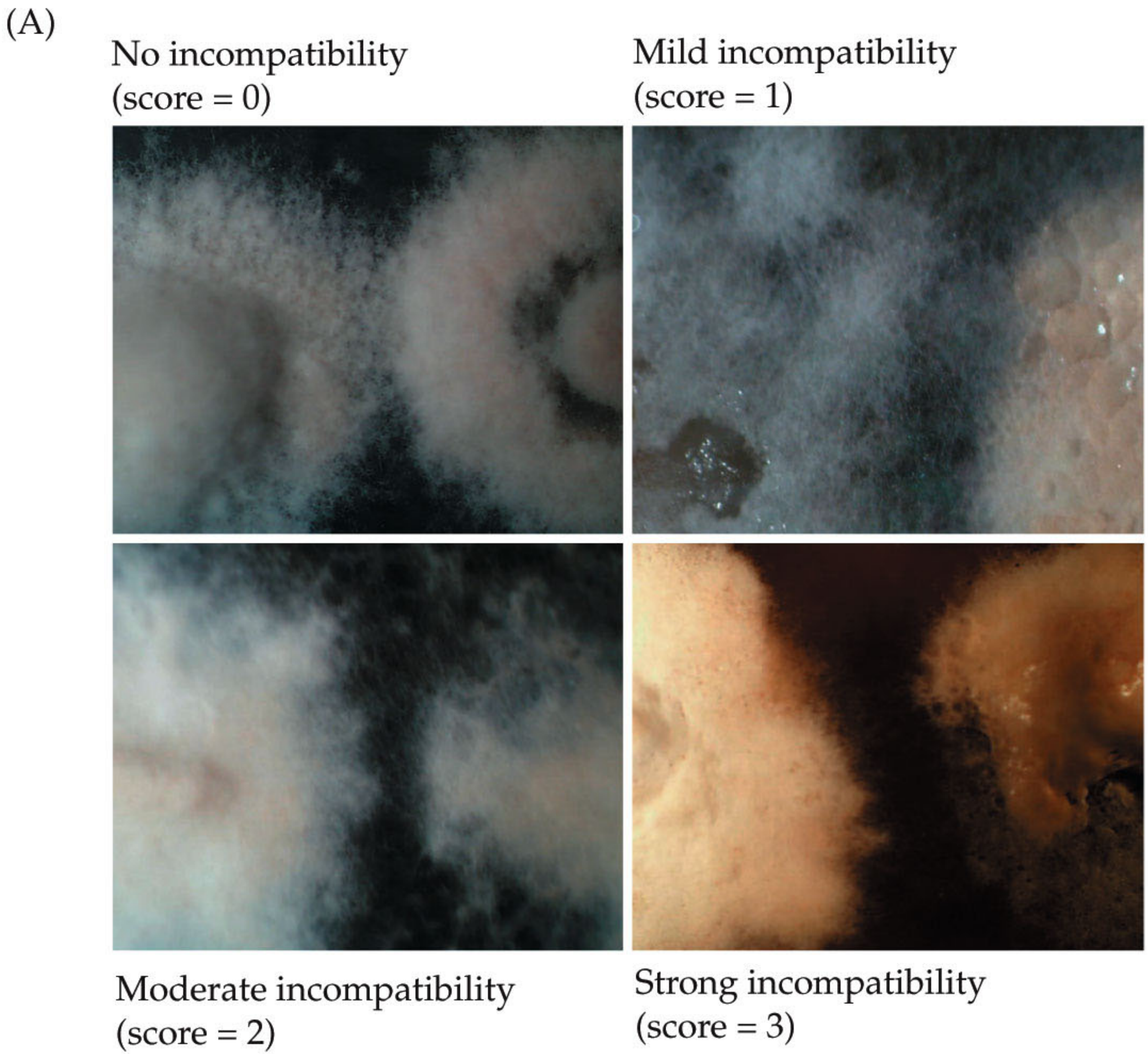
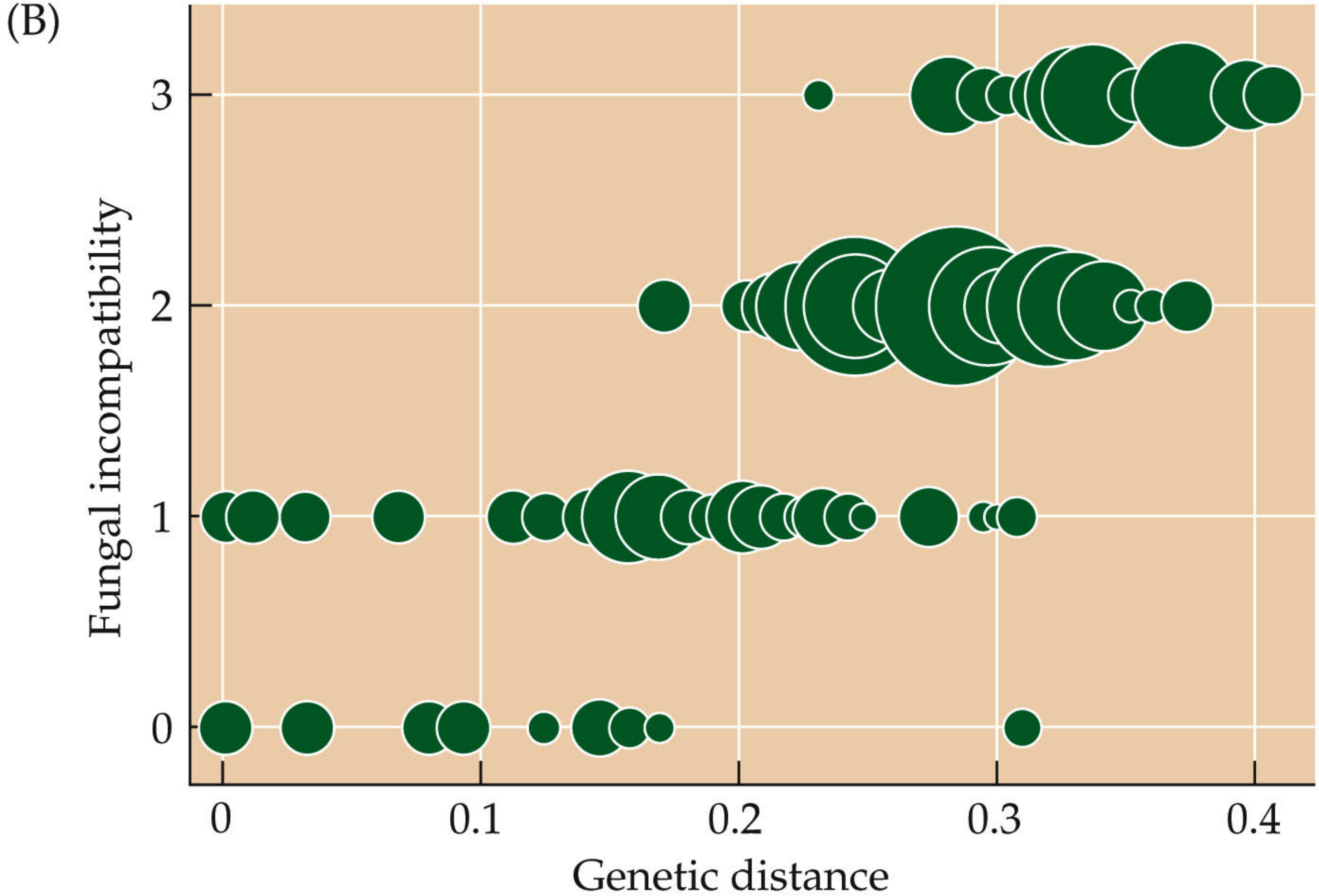


Figure 14.21 Resident Fungi Inhibit Foreign Fungi (Part 2)



Leaf-cutter ants are potent herbivores and can be a pest of human agriculture.

These ants tend to increase in abundance after a forest is cut. This may be one reason that farms in some tropical regions are often abandoned after just a few years.

Leaf-cutter ants also introduce large amounts of organic matter into tropical forest soils.

Thus, they affect nutrient supply and cycling in the forest.

Ant refuse areas contain about 48 times the nutrients found in leaf litter.

Plants increase their production of fine roots in ant refuse areas.

Although leaf-cutter ants reduce net primary productivity (NPP) by harvesting leaves, some of the other activities (tillage, fertilization) may increase NPP.

The net effect of the ants on NPP is difficult to estimate.

Other intriguing questions remain.

Ecologists sometimes fall through the soil, landing in what appear to be empty ant chambers.

Are they abandoned ant chambers? If so why were they abandoned? Why don’t plant roots proliferate there?

As we learn more, new questions always arise.