

17

Biogeography



- *Case Study*: The Largest Ecological Experiment on Earth
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- *Connections in Nature*: Human Benefits of Tropical Rainforest Diversity

Case Study: The Largest Ecological Experiment on Earth

One hectare of rainforest in the Amazon contains more plant species than all of Europe!

The Amazon Basin is the largest watershed in the world. The number of fish species in the Amazon River exceeds the total number found in the entire Atlantic Ocean.

Figure 17.1 Diversity Abounds in the Amazon



Case Study: The Largest Ecological Experiment on Earth

When these ecosystems are disturbed, there is devastating species loss.

Deforestation began with road building in the 1960s.

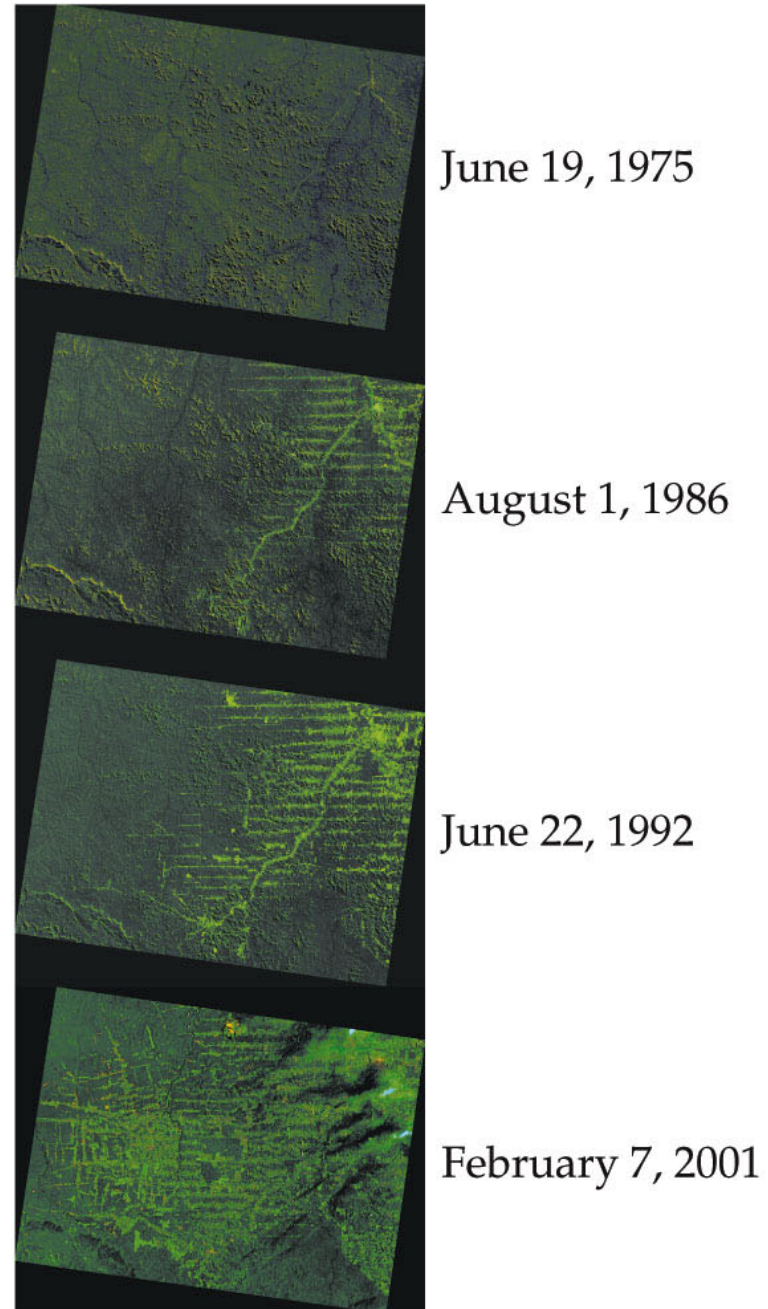
In 50 years' time, 15% of the rainforest has been converted to pastureland, towns, roads, and mines.

Case Study: The Largest Ecological Experiment on Earth

While 15% seems modest, the sheer number of species impacted is staggering.

The pattern of deforestation has also resulted in extreme habitat fragmentation, making it more difficult to maintain species diversity.

Figure 3.6 Tropical Deforestation



Case Study: The Largest Ecological Experiment on Earth

In 1979, habitat fragmentation spurred Thomas Lovejoy to initiate the longest running ecological experiment ever conducted: The Dynamics of Forest Fragments Project (BDFFP).

He was guided by *The Theory of Island Biogeography*, an explanation for the observation that more species are found on large islands than on small islands.

Case Study: The Largest Ecological Experiment on Earth

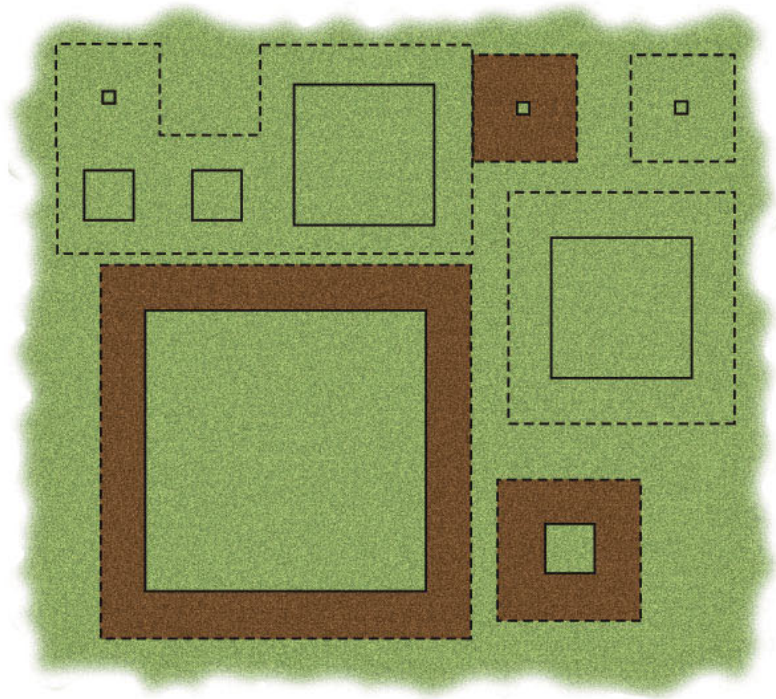
Four different sizes of forest plots were set up: 1, 10, 100, or 1,000 hectares.

Control plots were surrounded by forest. Fragments were surrounded by logged land.

The BDFFP started with the question, “What is the minimum area of rainforest needed to maintain species diversity?”

Figure 17.2 Studying Habitat Fragmentation in Tropical Rainforests

(A)



(B)



Physical factors and species interactions are important regulators of species distributions on local scales.

But global and regional scale processes are also important in determining the distributions and diversity of species on Earth.

Biogeography and Spatial Scale

Concept 17.1: Patterns of species diversity and distribution vary at global, regional, and local spatial scales.

Biogeography is the study of patterns of species composition and diversity across geographic locations.

Biogeography and Spatial Scale

A tour of the forest biomes of the world reveals the huge variation in species richness and composition.

The Amazon rainforest is the most species-rich forest in the world, with approximately 1,300 tree species.

In contrast, the boreal forests of Canada have only 2 tree species that cover vast areas.

Figure 17.3 Forests around the World



TABLE 17.1**Tree Species Richness in Different Forests around the World**

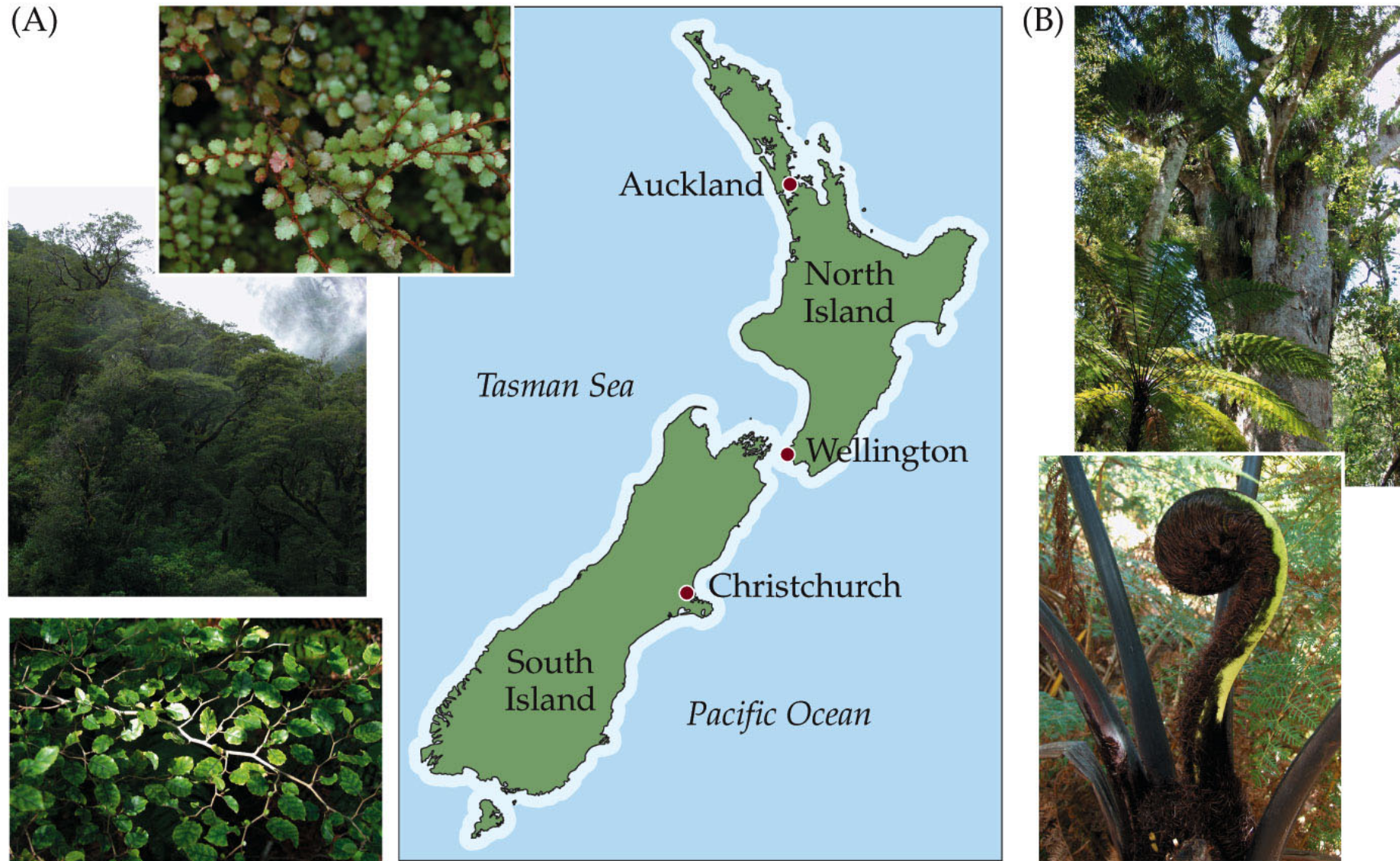
Forest location/ forest type	Latitude, longitude	Approximate tree species richness	Source
<i>Amazon, Brazil</i>	4°S, 60°W	1,300	Laurance 2001
<i>Southern California, USA</i>	35°N, 125°W	57	Allen et al. 2007
<i>Pacific Northwest, USA</i>			Franklin and Dyrness 1988
Douglas fir forest	45°N, 123°W	7	
Garry oak forest	45°N, 123°W	4	
<i>Boreal forest, Canada</i>	64°N, 125°W	2	Kricher 1998
<i>New Zealand</i>			Dawson and Lucas 2000
Beech forest	45°S, 170°E	20	
Flowering tree forest	35°S, 170°E	100	

Biogeography and Spatial Scale

New Zealand has been separated from continental land masses for about 80 million years. Since that time evolution has resulted in unique forests.

About 80% of the species are **endemic**, meaning that they occur nowhere else on Earth.

Figure 17.4 Forests of North and South Island, New Zealand



Biogeography and Spatial Scale

Even within New Zealand there is a range of tree species composition and richness.

North Island is warmer, with many flowering tree species, and some emergent conifers.

The kauri (*Agathis australis*) is among the largest tree species on Earth.

Biogeography and Spatial Scale

The kauri trees have been extensively logged, and exist in only two small reserves.

Old-growth stands of kauris take 1,000–2,000 years to generate, so these forests are irreplaceable to modern society.

The forest tour reveals several patterns:

- Species richness and composition vary with latitude.
- In general, the lower tropical latitudes have many more, and different, species than the higher temperate and polar latitudes.

Biogeography and Spatial Scale

- Species richness and composition also vary from continent to continent, even where longitude or latitude is roughly similar.
- The same community type or biome can vary in species richness and composition depending on its location on Earth.

Biogeography and Spatial Scale

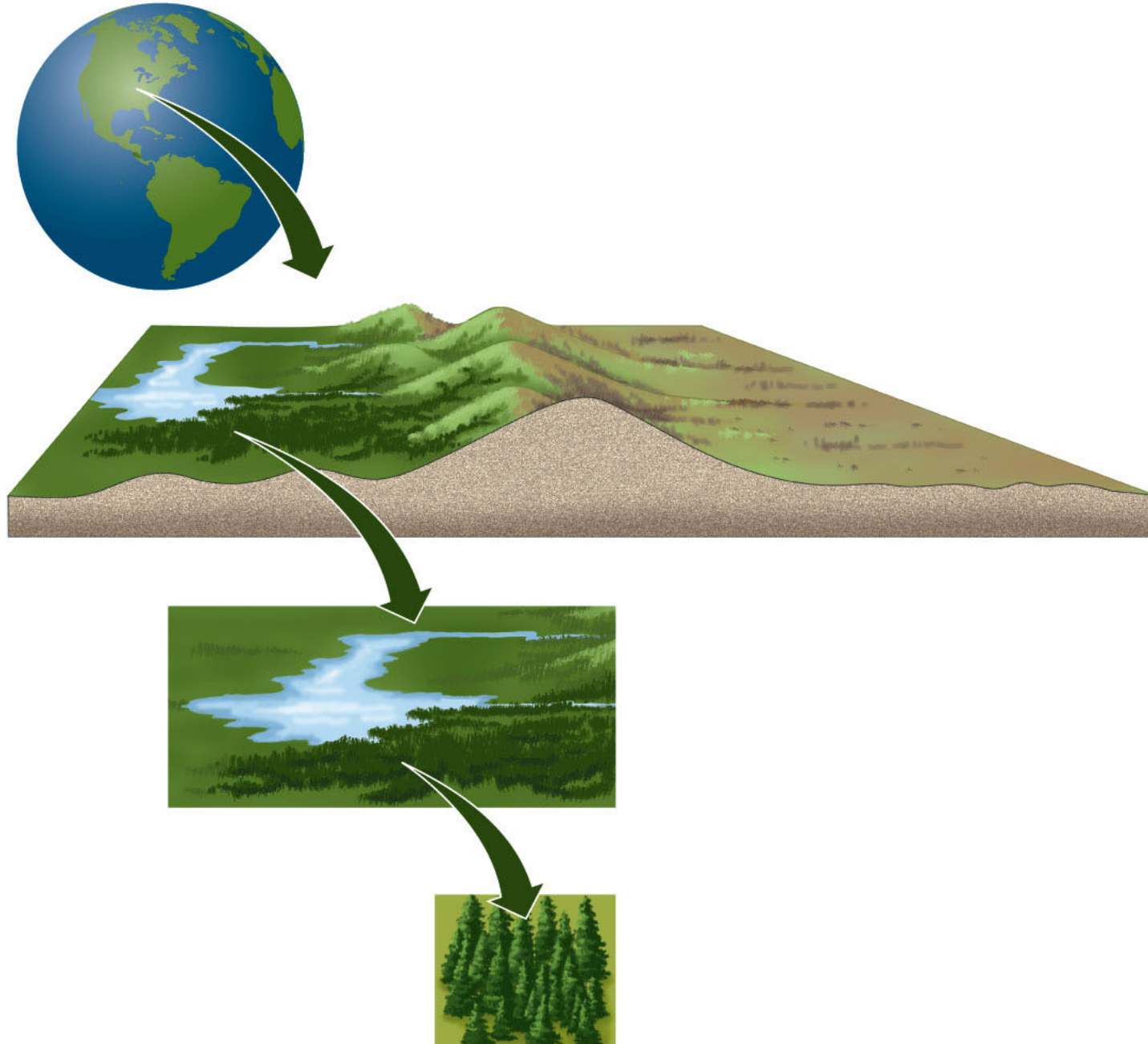
Ecologists have worked to understand the processes that control these broad patterns.

A number of hypotheses have been proposed, which are highly dependent on spatial scale.

Biogeography and Spatial Scale

Spatial scales are interconnected in a hierarchical way, with the patterns of species diversity and composition at one spatial scale setting the conditions for patterns at smaller spatial scales.

Figure 17.5 Interconnected Spatial Scales of Species Diversity



Global scale—the entire world.

- Species have been isolated from one another, on different continents or in different oceans, by long distances and over long periods.
- Rates of speciation, extinction, and migration help determine differences in species diversity and composition.

Biogeography and Spatial Scale

Regional scale—climate is roughly uniform and the species are bound by dispersal to that region.

Regional species pool—all the species contained within a region (**gamma diversity**).

Biogeography and Spatial Scale

Landscape—topographic and environmental features of a region.

Species composition and diversity vary within a region depending on how the landscape shapes rates of migration and extinction to and from critical local habitats.

Local scale—equivalent to a community.

Species physiology and interactions with other species weigh heavily in the resulting species diversity (**alpha diversity**).

Beta diversity—change in species number and composition, or *turnover* of species, as one moves from one community type to another.

Beta diversity represents the connection between local and regional scales of species diversity.

Biogeography and Spatial Scale

Actual area values of the different spatial scales depends on the species and communities of interest.

Example: Terrestrial plants might have a local scale of 10^2 – 10^4 m², but for phytoplankton, the local scale might be more like 10^2 cm².

Biogeography and Spatial Scale

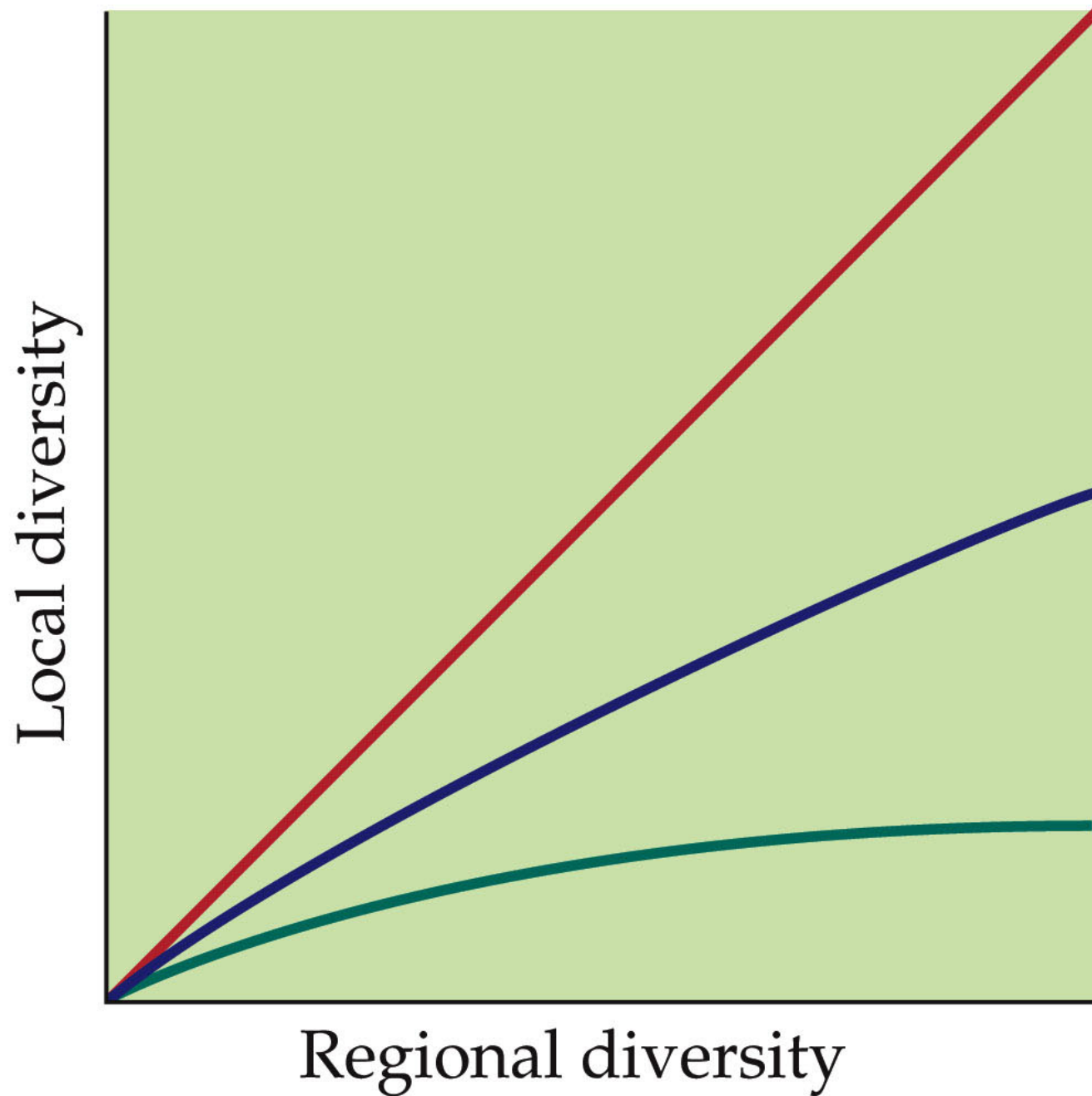
Patterns of species diversity, and the processes that control them, are interconnected across spatial scales.

The regional species pool provides the raw material for local assemblages and sets the theoretical upper limit on species diversity for communities.

Three types of relationships between local and regional diversity:

1. When regional and local species diversity are equal (slope = 1), all species in a region will be found in all communities. This is not really likely, as regions will always have landscape and habitat features that exclude some species from some communities.

Figure 17.6 What Determines Local Species Diversity?



Biogeography and Spatial Scale

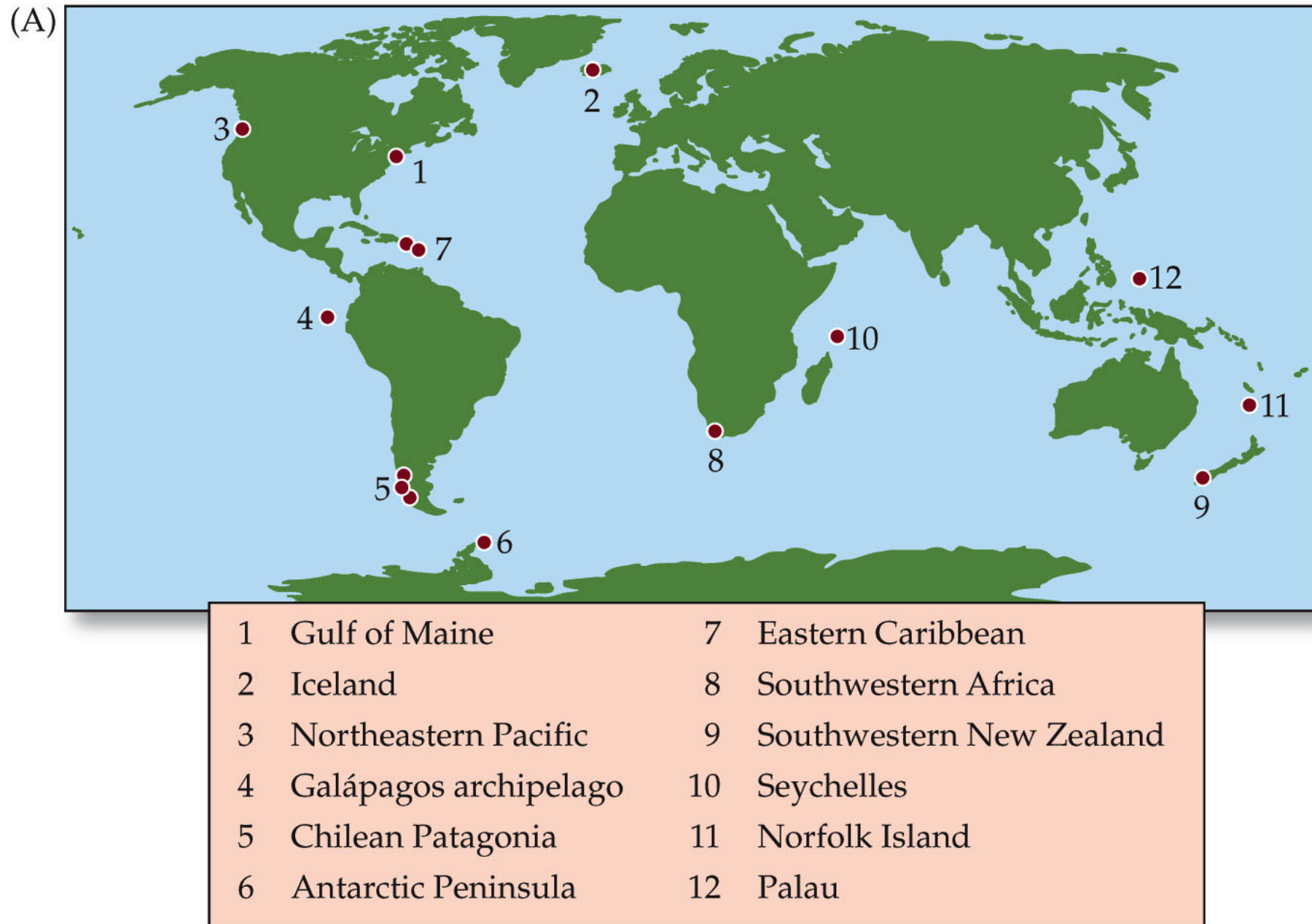
2. If local species richness is simply proportional to regional species richness, community species richness is largely determined by the regional species pool.
3. If local species richness levels off despite a large regional species pool, then local processes can be assumed to limit local species diversity.

Biogeography and Spatial Scale

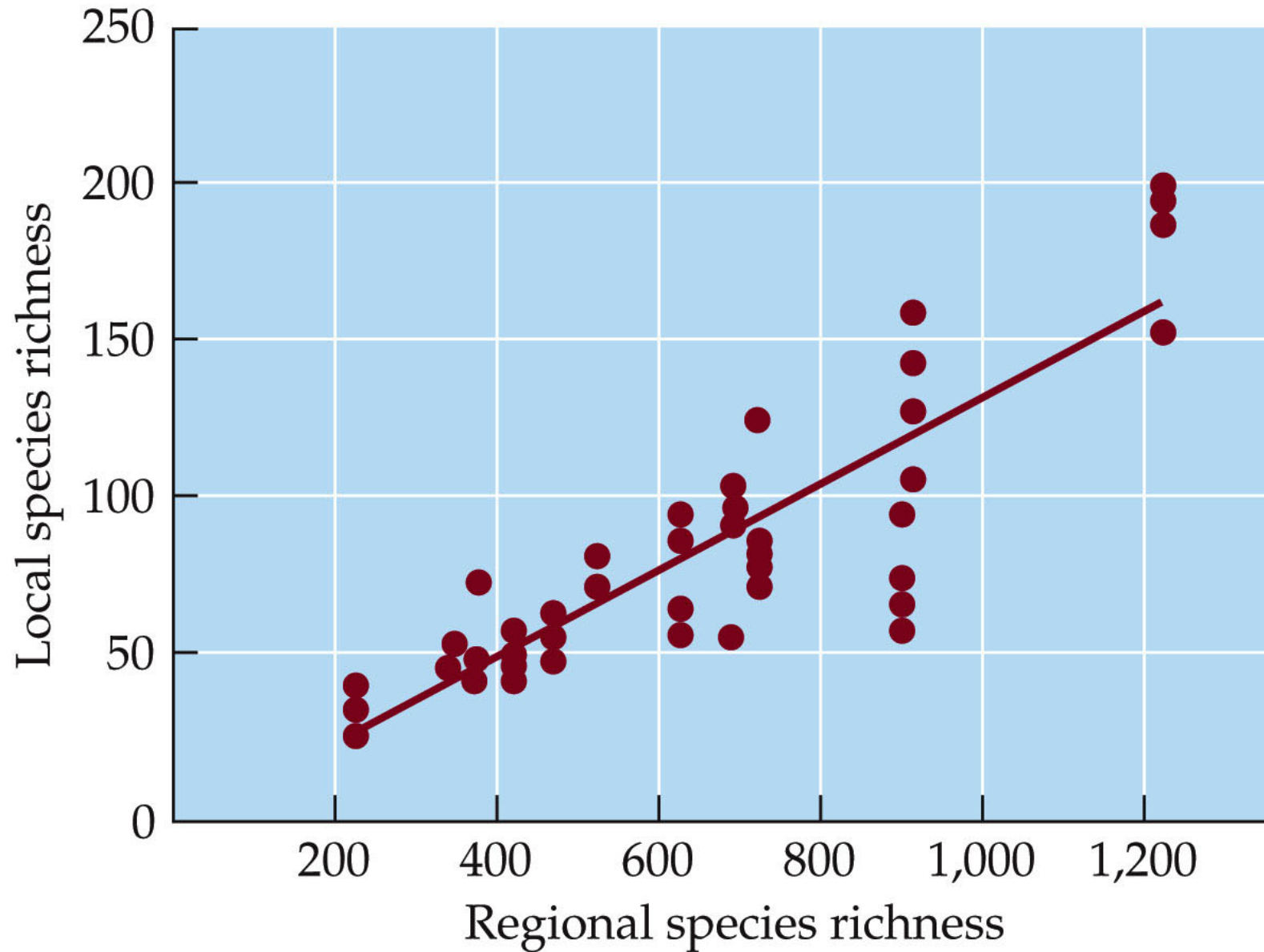
Witman et al. (2004) looked at invertebrate communities on subtidal rock walls at 49 local sites in 12 regions around the world.

A plot of all local sites showed that local species richness was always proportionally lower than regional species richness and that it never leveled off.

Figure 17.7 Marine Invertebrate Communities May Be Limited by Regional Processes (Part 1)



(B)



Biogeography and Spatial Scale

Regional species richness explained 75% of the variation in local species richness.

But this does not mean that local processes are unimportant.

There is still considerable unexplained variation that could be attributable to the effects of local processes.

Biogeography and Spatial Scale

The effects of species interactions, in particular, are likely to be highly sensitive to the local spatial scale chosen.

Inappropriate (usually too large) spatial scales are unlikely to detect local effects.

Concept 17.2: Global patterns of species diversity and composition are controlled by geographic area and isolation, evolutionary history, and global climate.

Biogeography was born with scientific exploration in the 19th century.

Alfred Russel Wallace (1823–1913) rightly earned his place as the father of biogeography.

Figure 17.8 Alfred Russel Wallace and His Collections

(A)



(B)



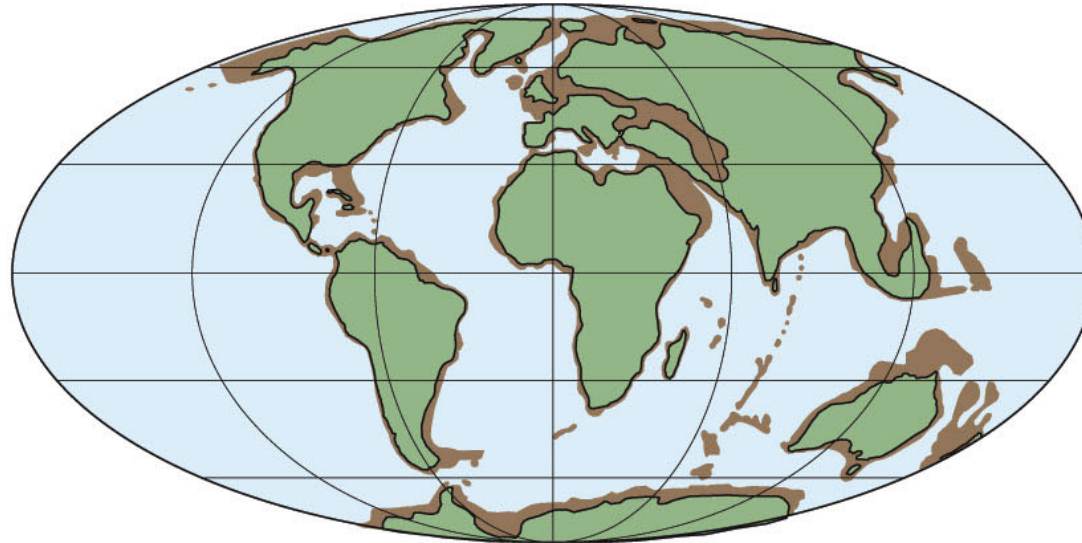
Wallace is best known, along with Charles Darwin, as the codiscoverer of the principles of natural selection.

But his main contribution was the study of species distributions across large spatial scales.

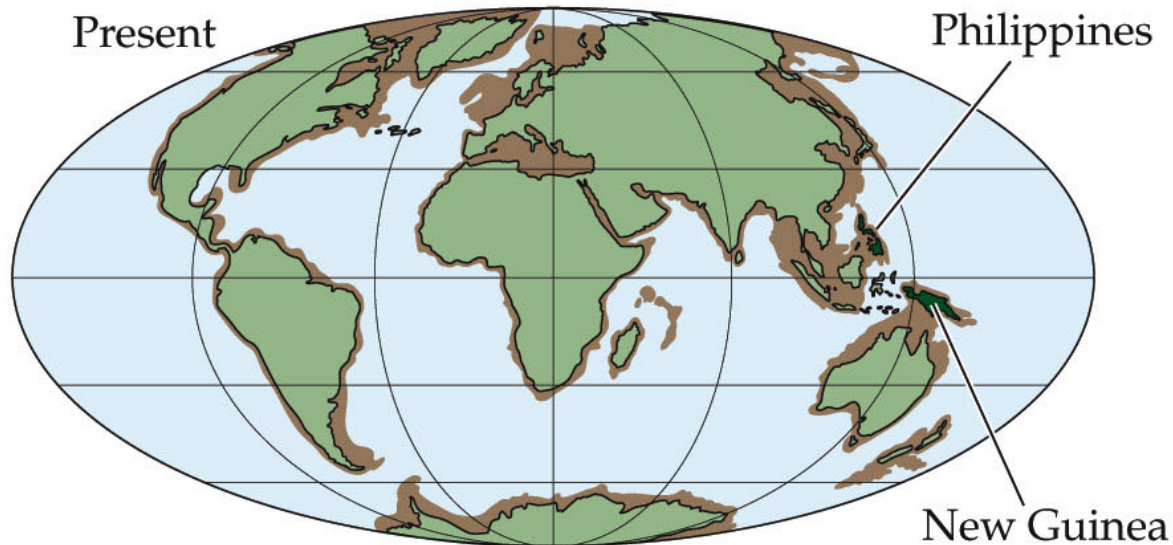
While working in the Malay Archipelago, Wallace noticed that the mammals of the Philippines were more similar to those in Africa (5,500 km away) than they were to those in New Guinea (750 km away).

Figure 8.10 Continental Drift Affects the Distribution of Organisms

30 million years before present



Present

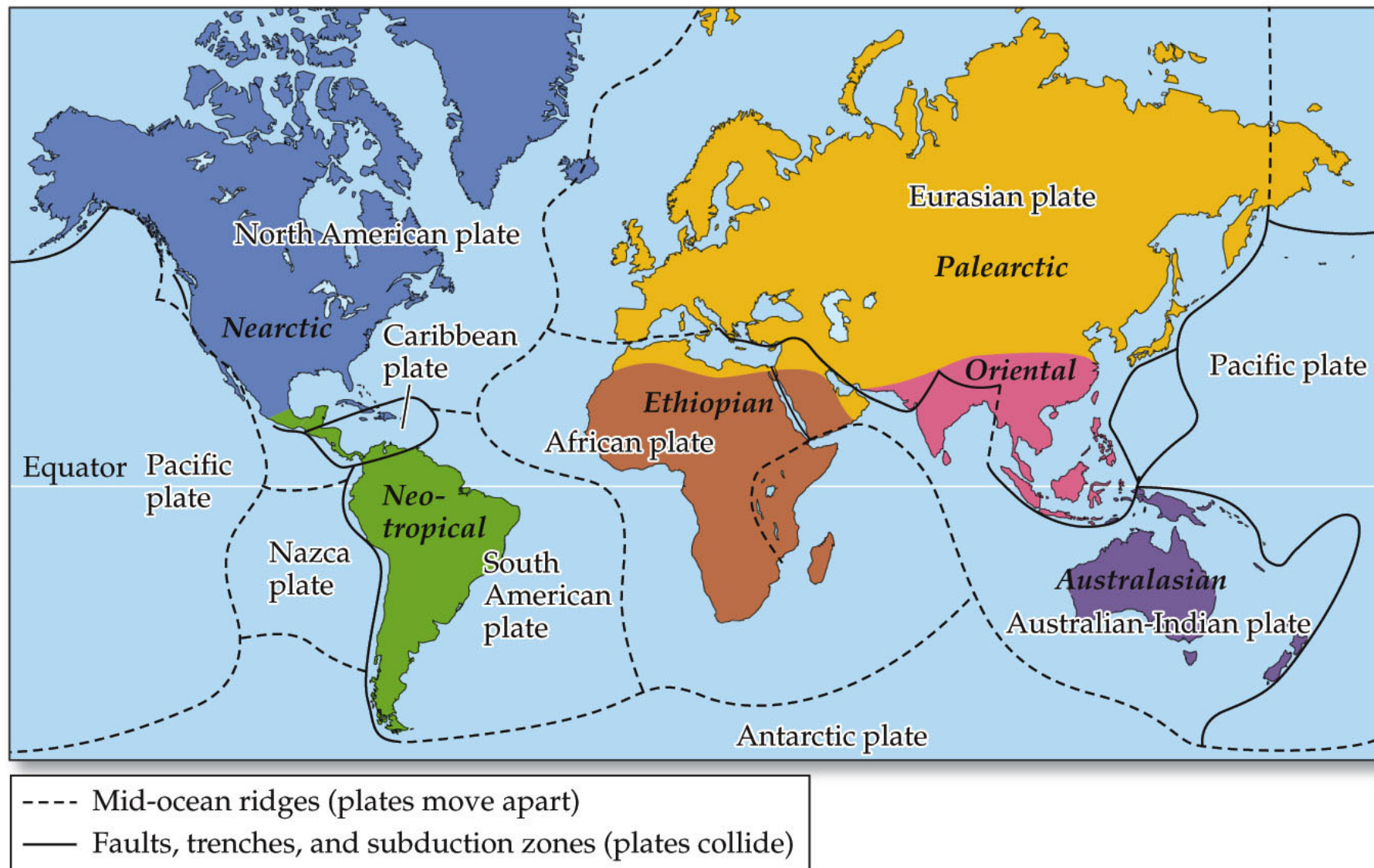


Wallace published *The Geographical Distribution of Animals* in 1876.

Wallace overlaid species distributions and geographic regions and revealed two important global patterns:

- Earth's land mass can be divided into six biogeographic regions.
- The gradient of species diversity with latitude.

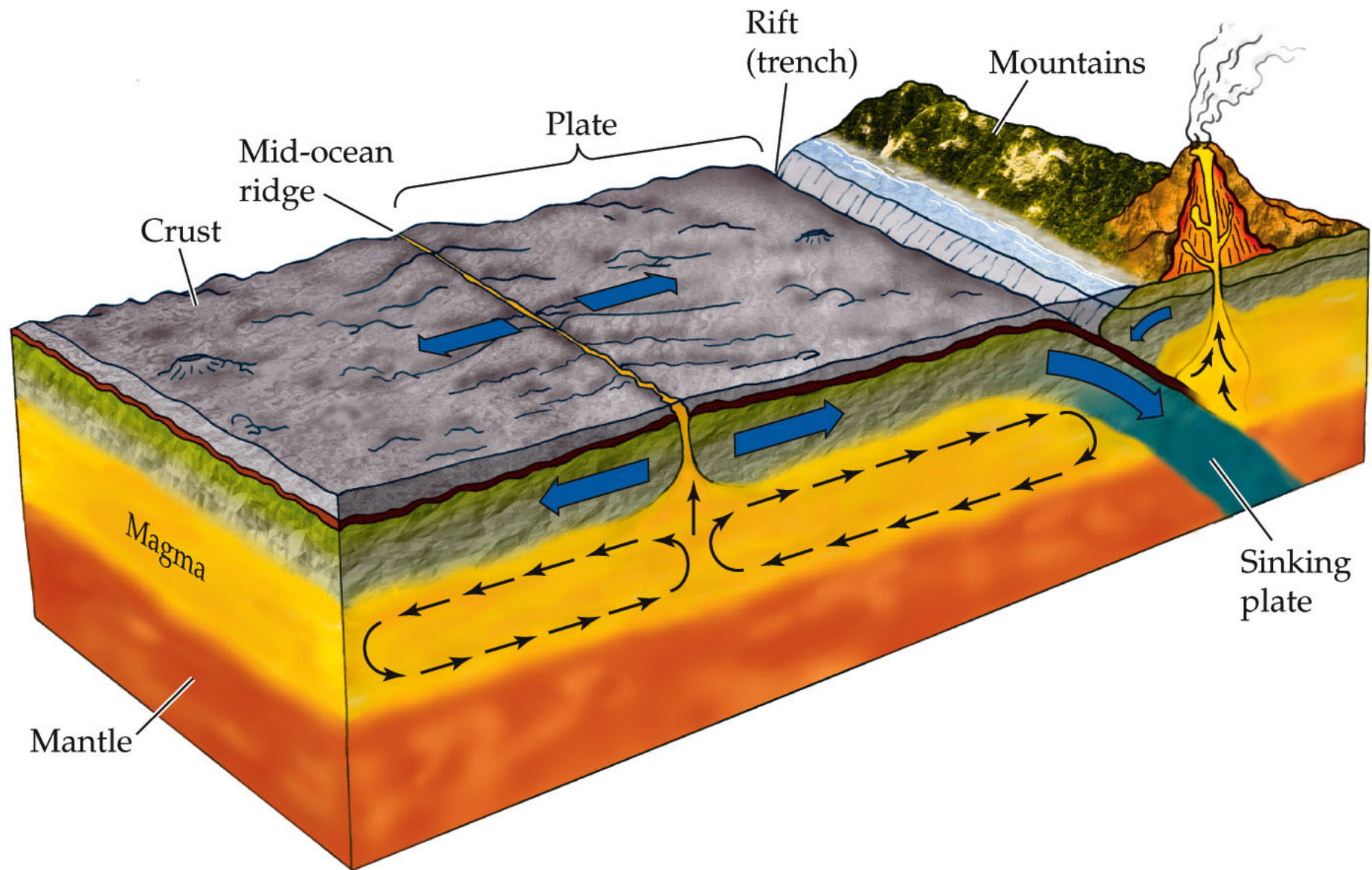
Figure 17.9 Six Biogeographic Regions



The six biogeographic regions correspond roughly to Earth's six major tectonic plates.

The plates are sections of Earth's crust that move or drift (**continental drift**) through the action of currents generated deep within the molten rock mantle.

Figure 17.10 Mechanisms of Continental Drift



At *mid-ocean ridges*, the molten rock flows out of the seams between plates and cools, creating new crust and forcing the plates to move apart.

At *subduction zones*, one plate is forced downward under another plate. These areas are associated with strong earthquakes, volcanic activity, and mountain range formation.

In other areas where two plates meet, the plates slide sideways past each other, forming a *fault*.

The positions of the plates, and the continents that sit on them, have changed dramatically over geologic time.

For biogeography, we will consider continental drift since the end of the Permian period, 250 million years ago.

At this time, all of Earth's land masses made up one large continent—Pangaea.

Pangaea first split into two land masses, Laurasia to the north and Gondwana to the south.

Gondwana separated into present-day South America, Africa, India, Antarctica, and Australia.

Laurasia eventually split up into North America, Europe, and Asia.

Some continents were separated from one another; others came together (e.g., India collided with Asia, forming the Himalayas).

Figure 17.11 The Positions of Continents and Oceans Have Changed over Geologic Time (Part 1)

(A)

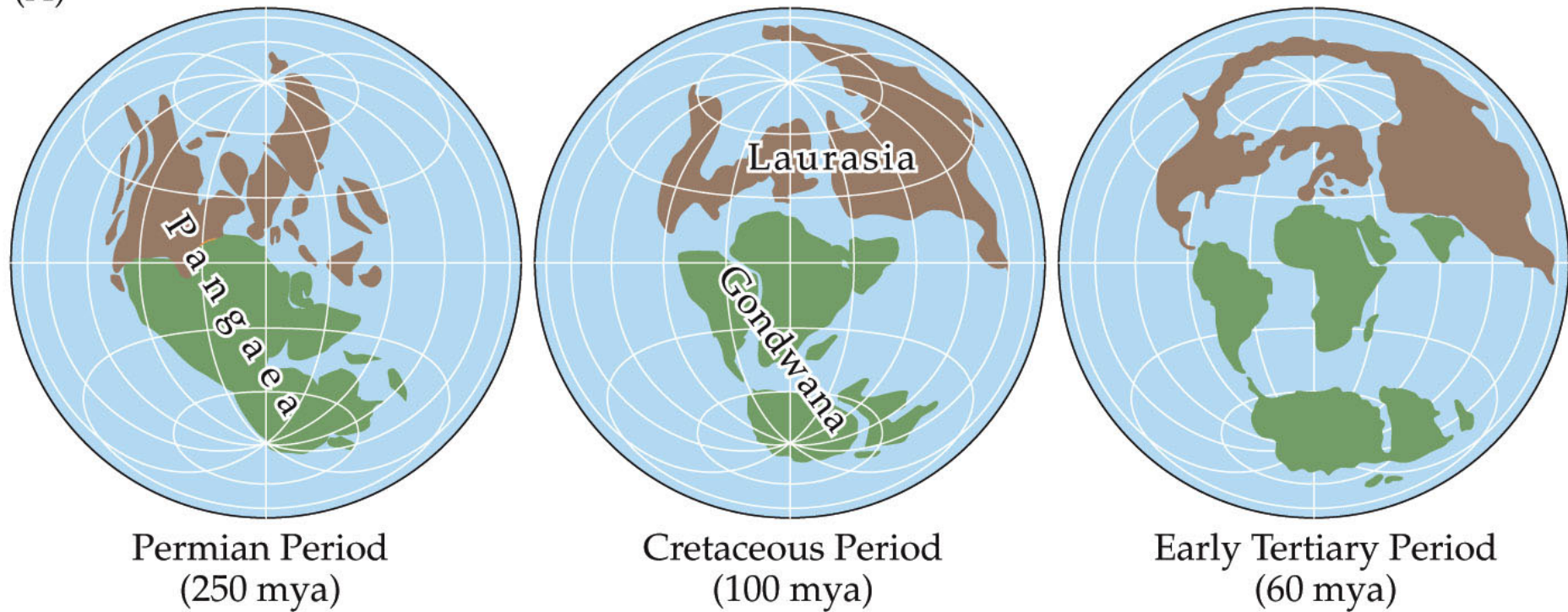
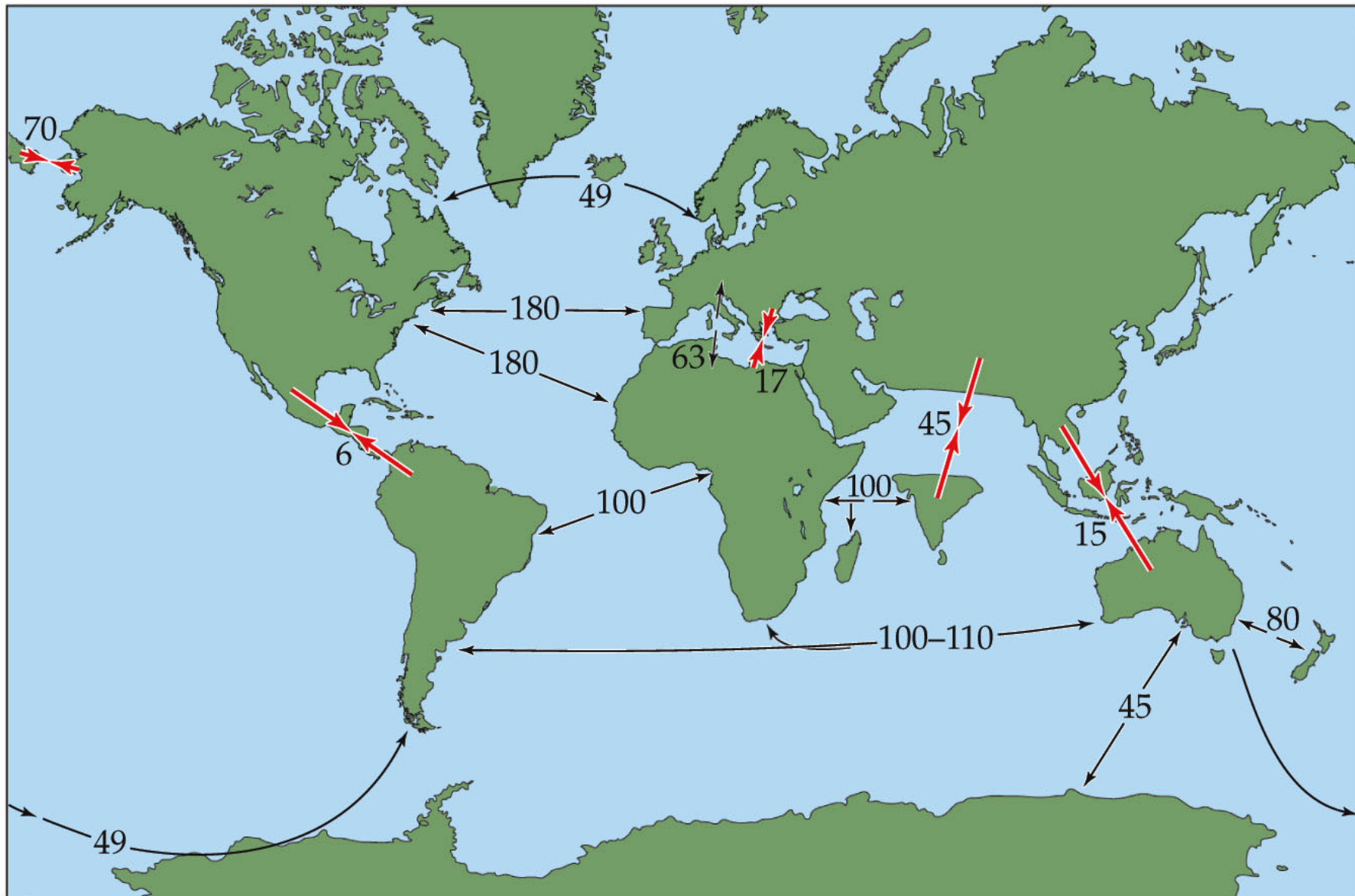


Figure 17.11 The Positions of Continents and Oceans Have Changed over Geologic Time (Part 2)

(B)



Continental drift has resulted in unique flora and fauna in some regions.

The Neotropical, Ethiopian, and Australian regions have been isolated for a long time and have very distinctive forms of life.

The Nearctic region differs substantially from the Neotropical region despite their modern-day proximity.

North America was part of Laurasia and South America was part of Gondwana, so they had no contact until about 3 million years ago.

Since then, there has been some movement of species from one continent to another.

The Nearctic and Palearctic, both part of ancient Laurasia, have similarities in biota across what is now Greenland as well as across the Bering Strait, where a land bridge has allowed exchanges of species over the last 100 million years.

The legacy of continental drift can be found in the fossil record and in existing taxonomic groups.

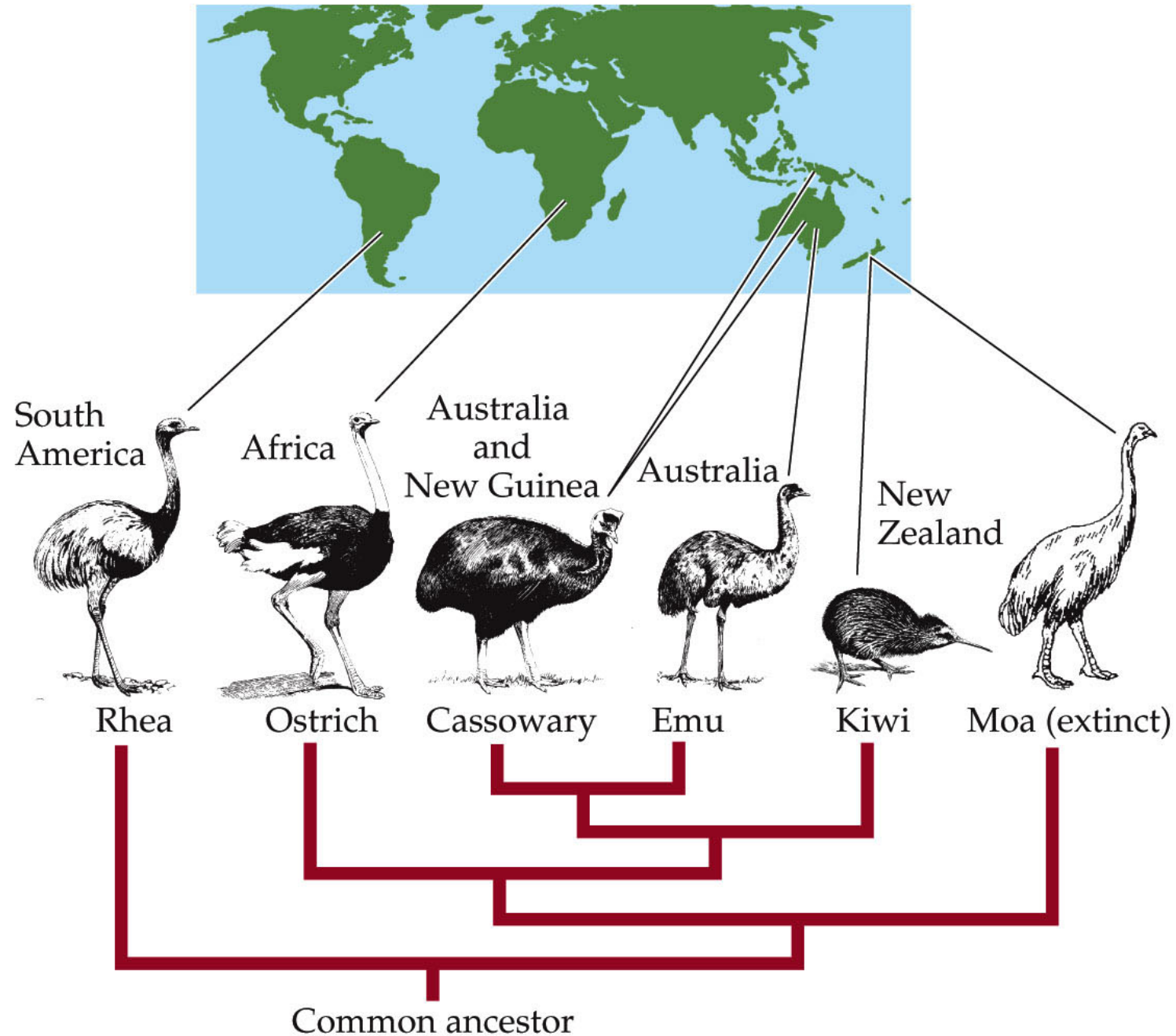
Vicariance—evolutionary separation of species due to a barrier such as continental drift.

Example: The large flightless birds (ratites) had a common ancestor from Gondwana.

The rheas of South America, ostriches of Africa, cassowaries and emus of Australia, and moas of New Zealand became isolated from one another.

They evolved unique characteristics in isolation, but retained their large size and inability to fly.

Figure 17.12 Vicariance among the Ratites



The kiwis of New Zealand are more closely related to ostriches, cassowaries, and emus than they are to moas, despite their co-occurrence with moas on New Zealand.

This suggests that kiwis evolved elsewhere and immigrated to New Zealand sometime after the breakup of Gondwana.

Tracing the threads of vicariance provided important evidence for early theories of evolution.

As Wallace began to amass more species and make geographic connections between them, his ideas about the origin of species started to solidify.

Oceans also have significant impediments to the exchange of biota, in the form of continents, currents, thermal gradients, and differences in water depth.

Identification of marine biogeographic regions has been hindered by the extra complicating factor of water depth and by the basic lack of knowledge of the deep oceans.

The latitudinal gradient in species diversity observed by Wallace has been documented repeatedly by studies over the last 200 years.

A pattern of longitudinal variation has also been observed.

Gaston et al. (1995) measured number of families along multiple transects running north to south.

While the number of families increased at low latitudes, longitude also had an effect. So-called *hot spots* or areas of high species richness occur at particular longitudes, sometimes secondary to latitude.

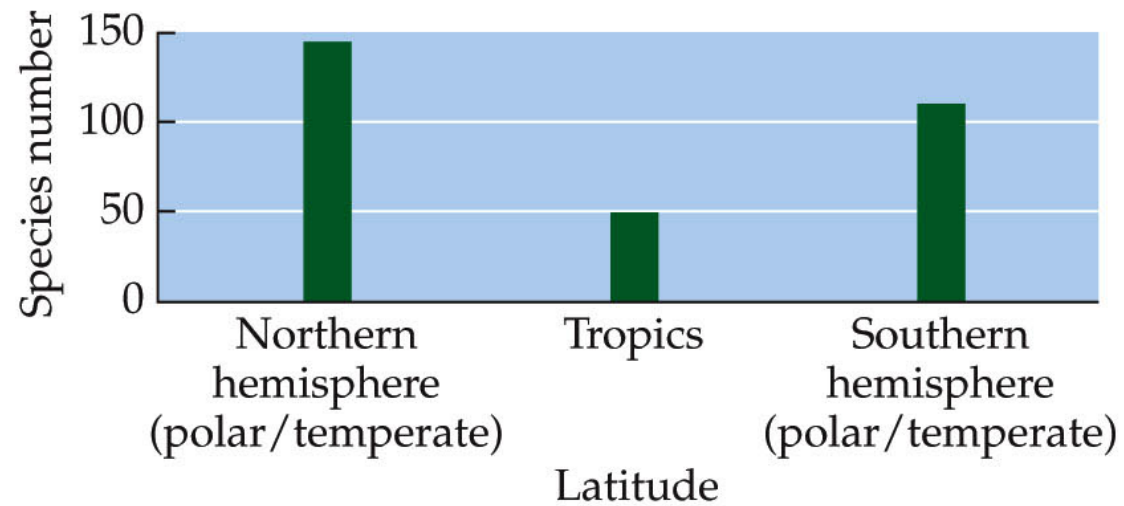
Some groups of organisms display the opposite pattern in latitudinal diversity.

Seabirds have highest density at temperate and polar latitudes.

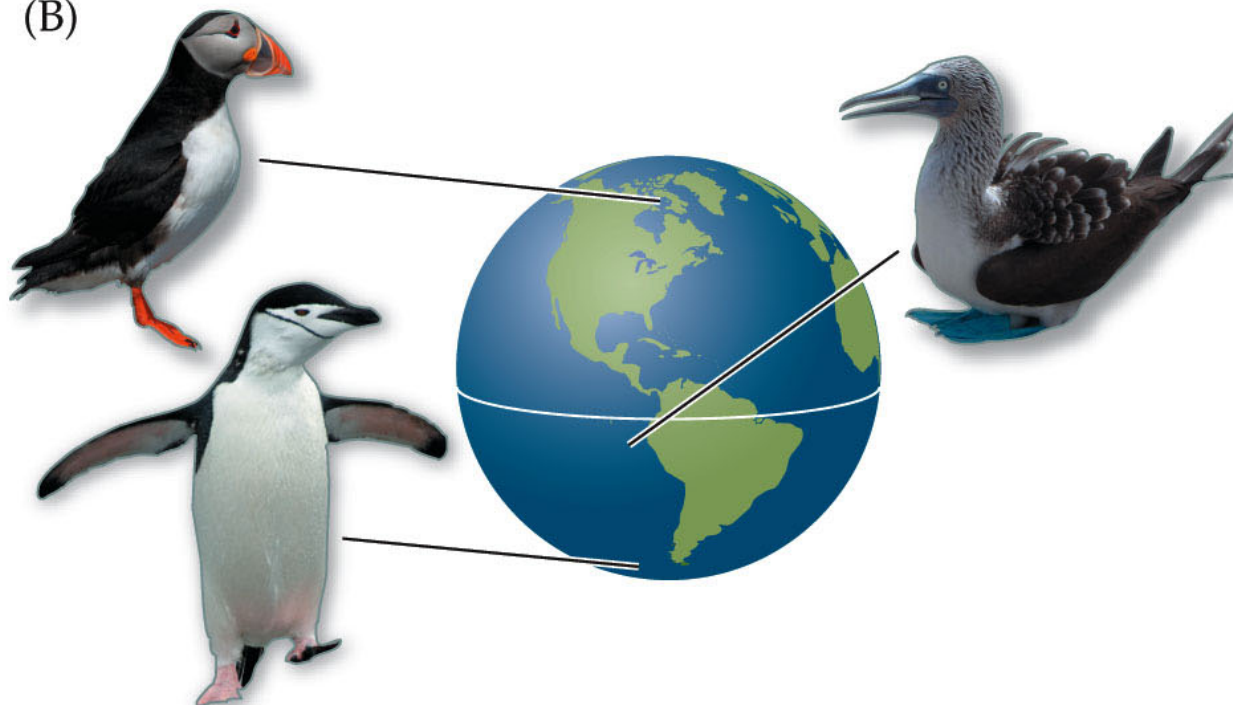
This pattern correlates with marine productivity, which is substantially higher in temperate and polar oceans.

Figure 17.14 Seabirds Go against Conventional Wisdom

(A) Global seabird diversity



(B)



The same pattern has been observed in marine benthic communities, which have much higher productivity at higher latitudes.

Productivity differences are one possible explanation for latitudinal gradients in species diversity.

Global patterns of species richness should be controlled by three processes: Speciation, extinction, and migration.

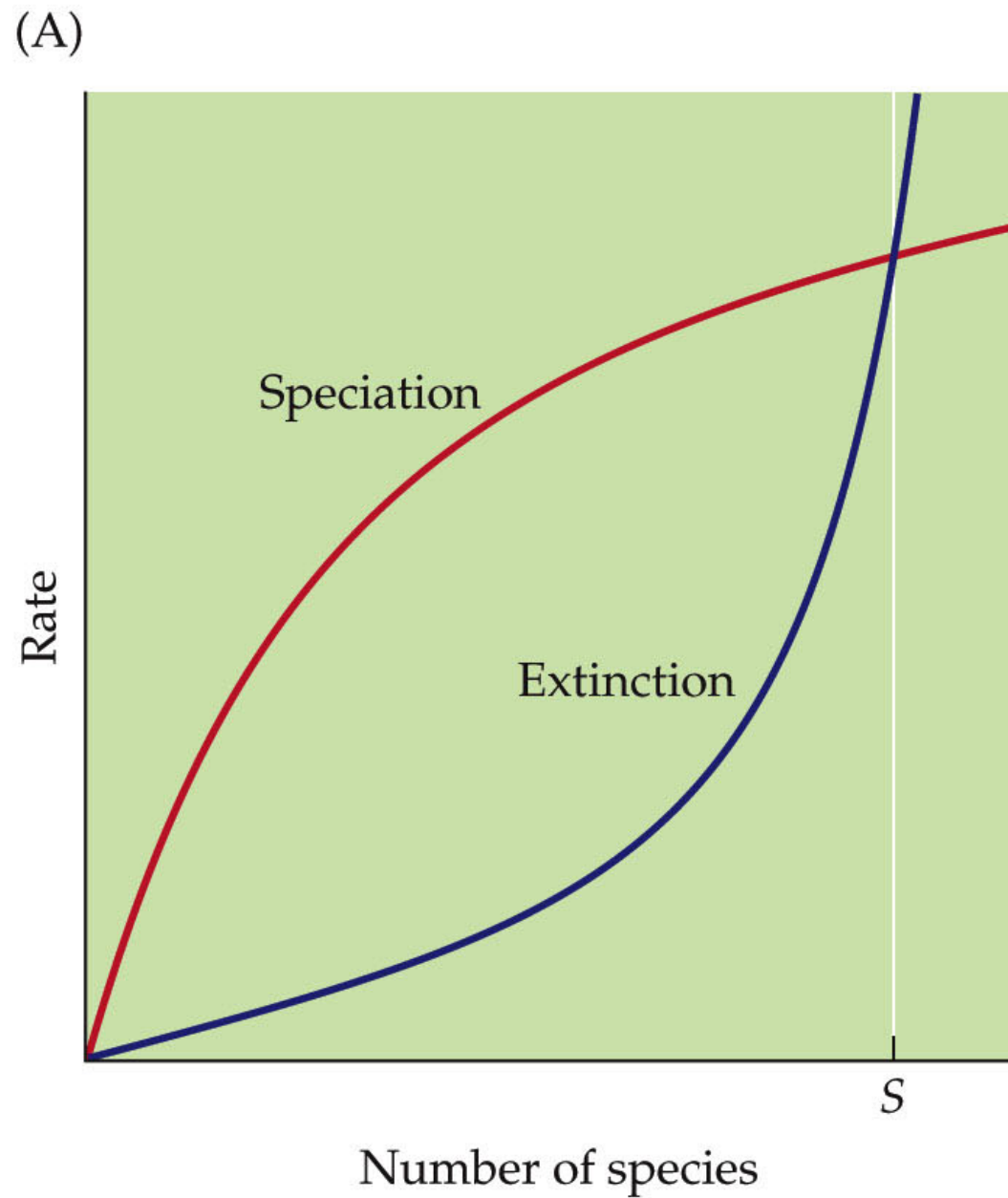
If we assume migration rates are similar everywhere, then species richness should reflect a balance between extinction and speciation.

Both speciation and extinction rates should increase with species richness.

As the number of species increases, we would expect more species to evolve from them (a positive feedback loop).

The probability of extinction would increase (the more species, the more extinctions), and more species would cause more resource depletion and thus extinctions.

Figure 17.15 A How Many Species?

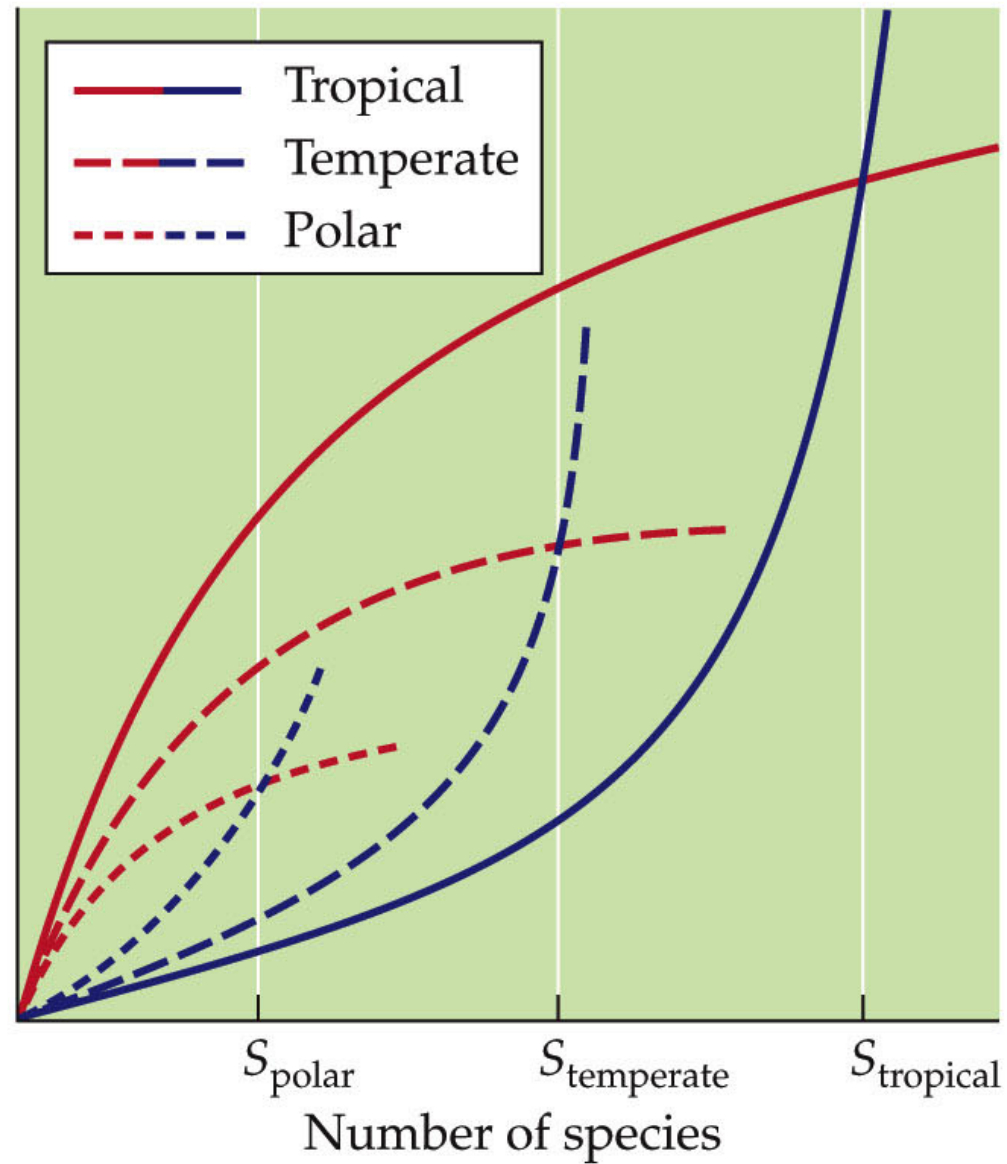


This model can then be used to make predictions about species richness at different latitudes.

Speciation and extinction rates should be highest in the tropics and lowest in the polar regions.

Figure 17.15 B How Many Species?

(B)



Is there an upper limit on the number of species?

Some ecologists have suggested that the number of ecological niches is endless, and in the absence of major global disturbance (e.g., climate change, meteorite impacts, etc.), there is no reason why global species diversity could not continue to increase indefinitely.

What ultimately controls the rates of speciation and extinction?

There are many hypotheses. One difficulty: Multiple and confounding gradients in geographic area, evolutionary age, and climate that are correlated with species diversity gradients.

The global scale makes manipulative experiments impossible.

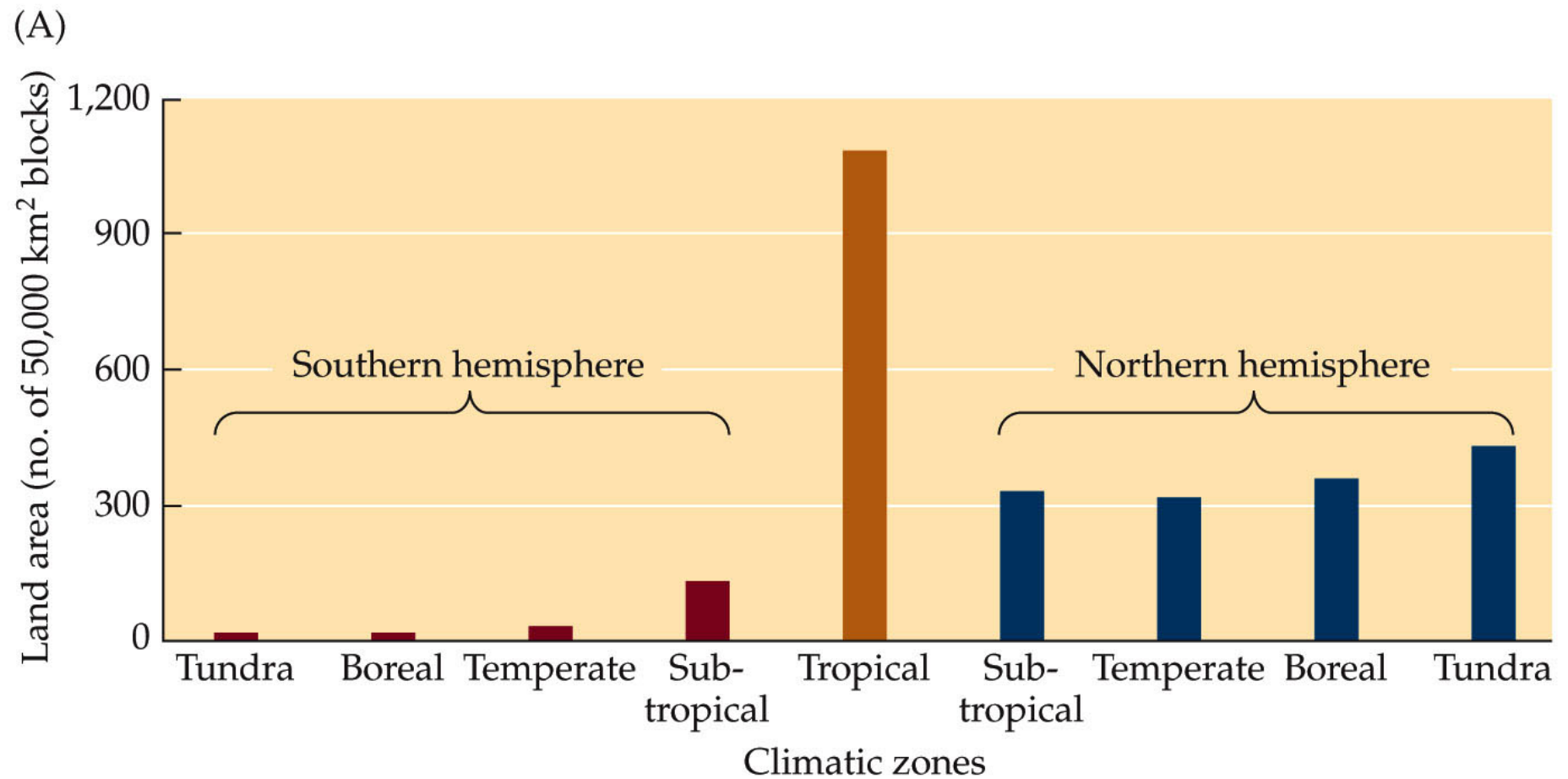
It is clear that the factors that drive these rates are not mutually exclusive, but interact to produce the gradients we see.

Temperature hypothesis:

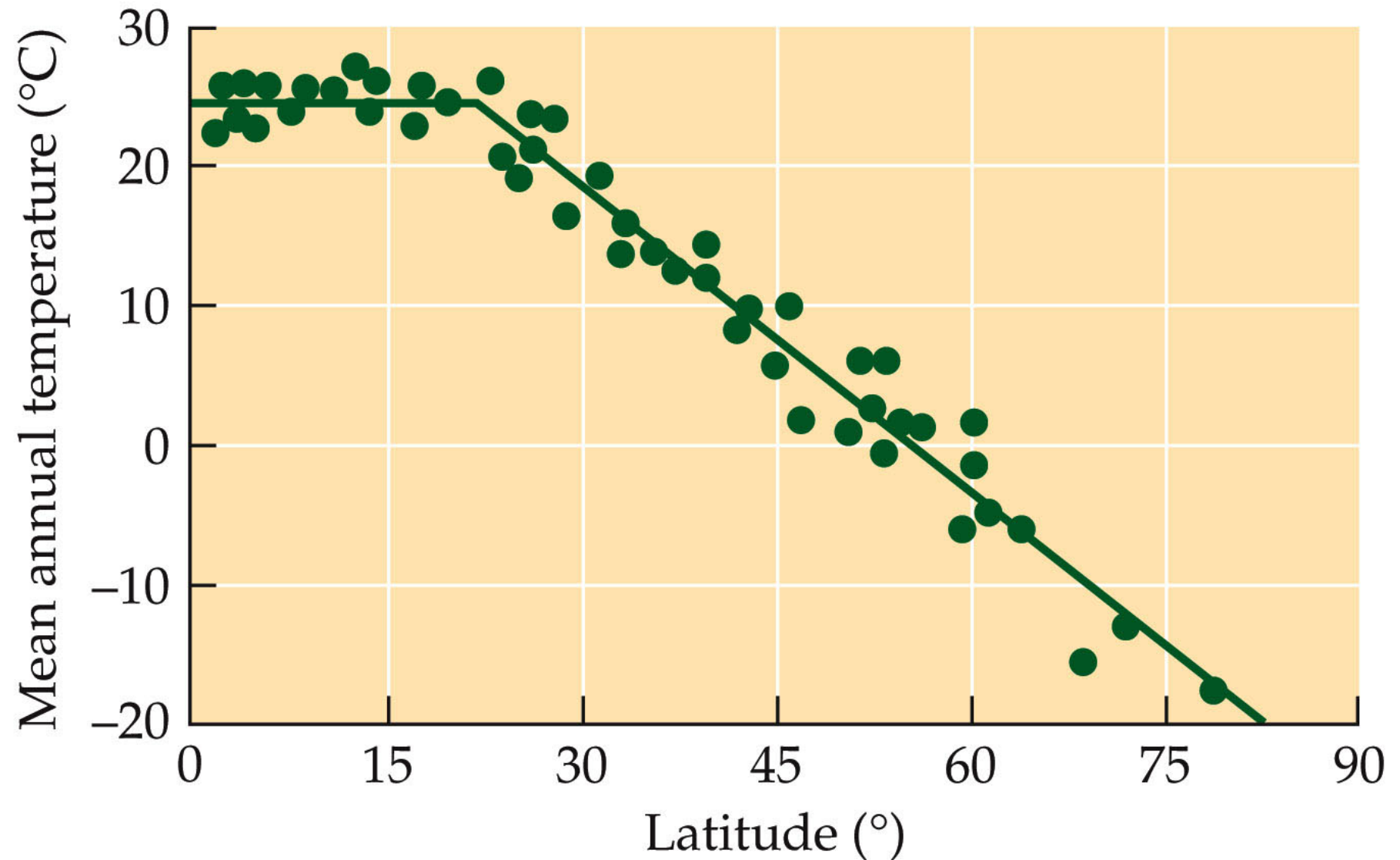
Terrestrial species diversity is highest in the tropics because the tropics have more land area than other latitudes.

This area is also the most thermally stable—temperatures remain uniform year-round.

Figure 17.16 Do Land Area and Temperature Influence Species Diversity? (Part 1)



(B)



Rosenzweig (1992) argued that a larger and more thermally stable area should decrease extinction rates in two ways:

- Increased population sizes decreases the chance of extinction.
- Increased geographic ranges also reduces risk of extinction.

Species with large geographic ranges would also have greater chance of geographic isolation and speciation.

Evolutionary history hypothesis:

Tropical regions have longer histories, they have been climatically stable and thus had a lot of time for evolution to occur.

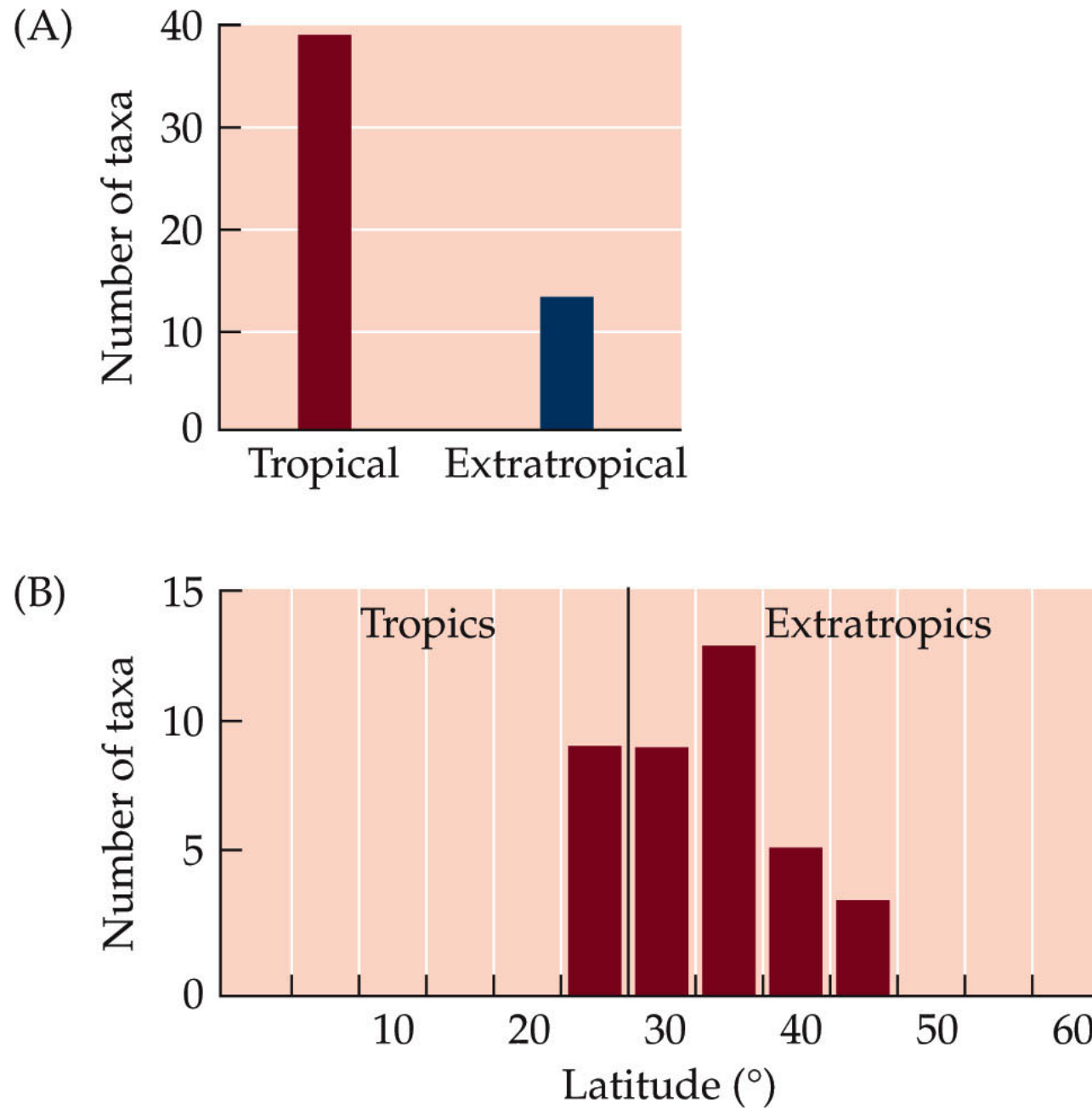
At higher latitudes, severe climatic conditions such as ice ages would increase extinction rates and hinder speciation.

This is supported by a study of modern and fossil marine bivalves (Jablonski et al. 2006).

Most extant taxa originated in the tropics and spread toward the poles.

Thus the tropics could be seen as a “cradle” of diversity. But they can also be a “museum”—species that diversify there tend to stay there.

Figure 17.17 The Tropics Are a Cradle and Museum for Speciation



The current loss of biodiversity in the tropics will have profound effects.

It compromises species richness today, and could also cut off the supply of new species to higher latitudes in the future.

Productivity hypotheses:

For terrestrial systems, species diversity is higher in the tropics because productivity is higher.

Higher productivity should promote larger population sizes, which will lead to lower extinction rates.

Productivity can also explain the reverse pattern seen in sea birds.

But some very productive habitats, such as estuaries, have low species diversity.

This hypothesis will be considered further, at local scales of diversity.

Regional Biogeography

Concept 17.3: Regional differences of species diversity are controlled by area and distance due to a balance between immigration and extinction rates.

An important concept in biogeography is the relationship between species number and geographic area.

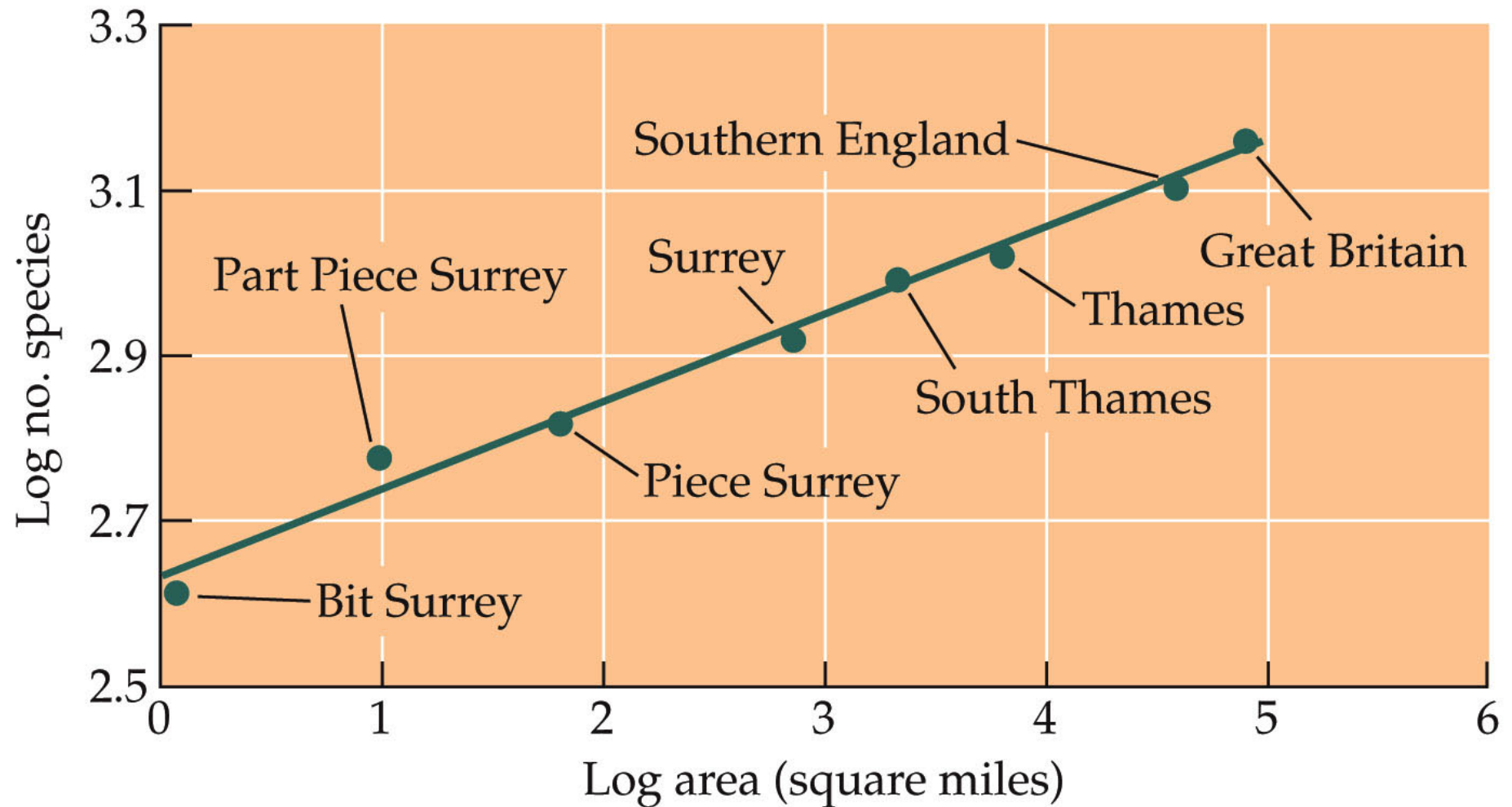
Species–area relationship—species richness increases with increasing area sampled.

Regional Biogeography

The first species–area curve was made for plants in Great Britain.

With each increase in area sampled, species richness increases until it reaches a maximum number bounded by the largest area considered.

Figure 17.18 The Species–Area Relationship



Box 17.1 Species–Area Curves

Species–area curves plot species richness (S) of a particular sample against the area (A) of that sample.

The relationship between S and A is estimated by linear regression:

$$S = zA + c$$

z = slope, c = y -intercept

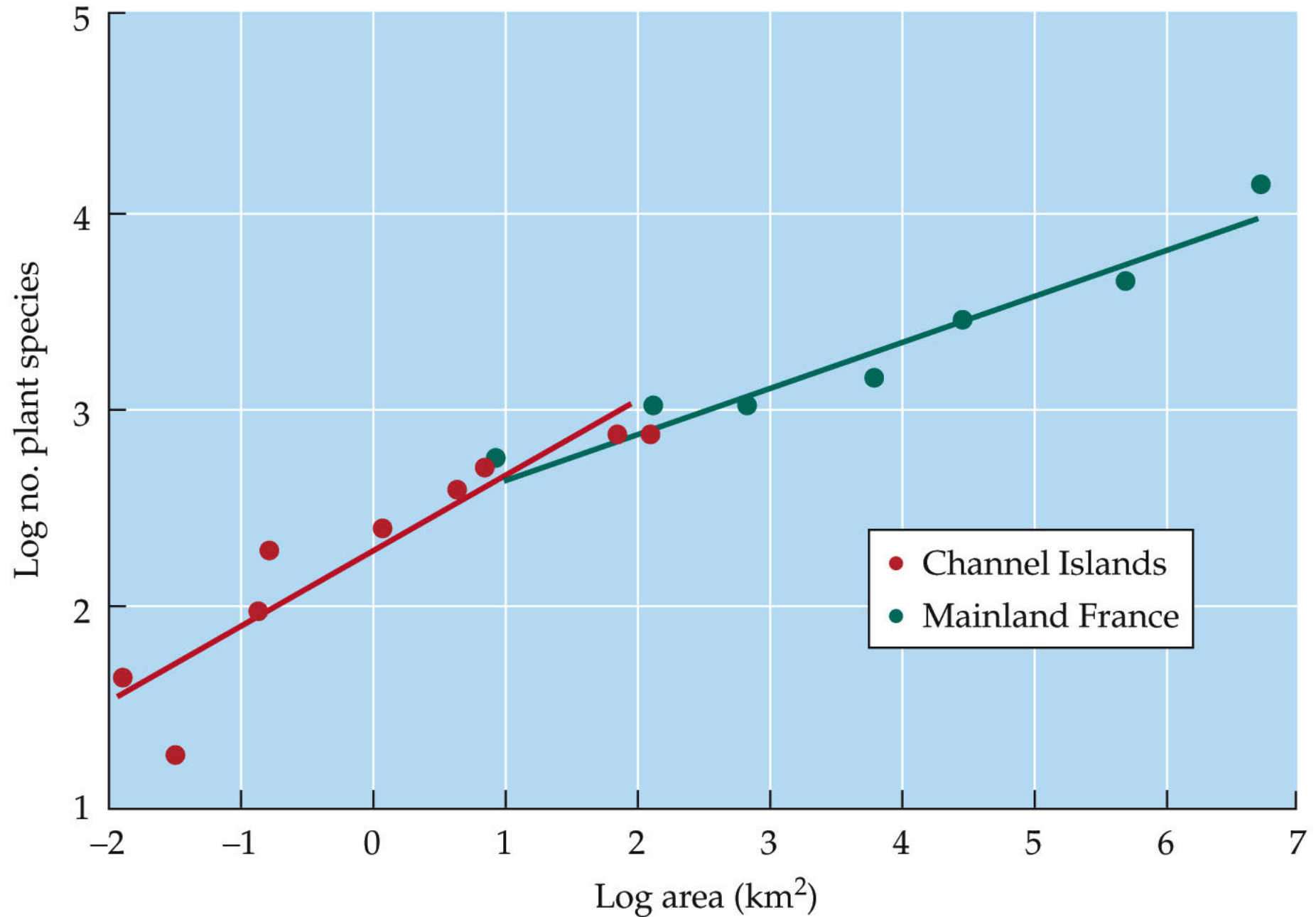
Box 17.1 Species–Area Curves

Species–area data are typically nonlinear, so S and A are transformed into logarithmic values so that the data fall on a straight line.

Species–area curves were plotted for plants on the Channel Islands and the French mainland. Curves for islands tend to have steeper slopes than those for mainlands.



Box 17.1, Figure A Species–Area Relationships of Island versus Mainland Areas (Part 2)



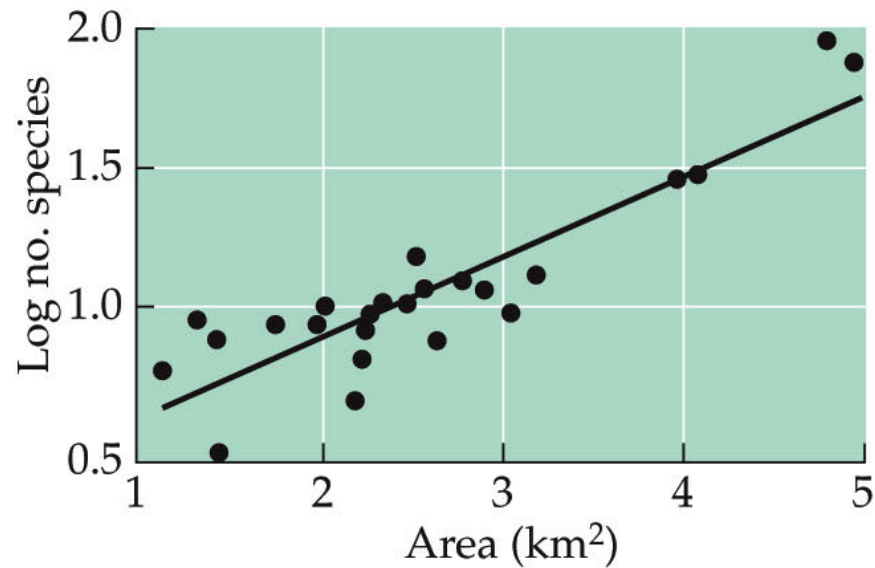
Islands include all kinds of isolated areas surrounded by dissimilar habitat (*matrix* habitat).

Habitat fragments, such as in the Amazon forest, can be considered as islands.

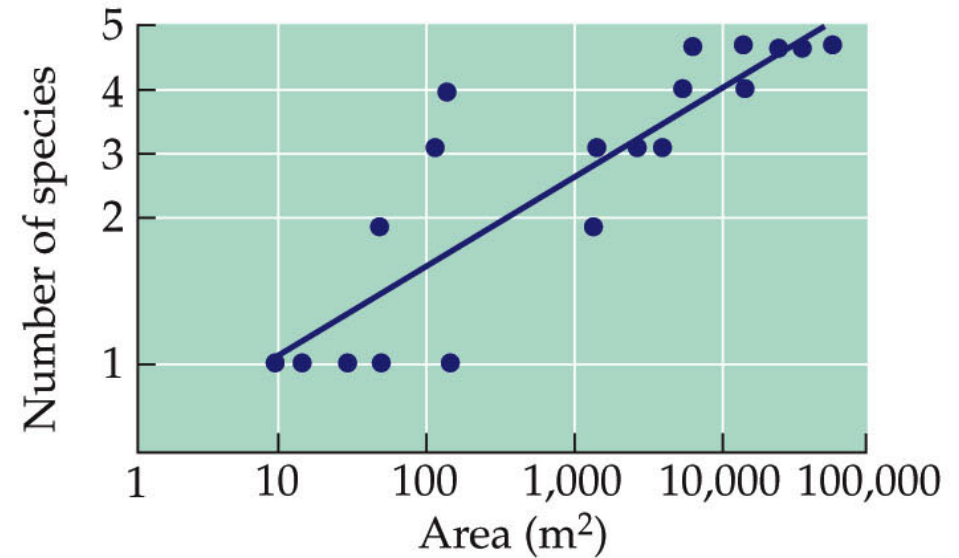
All display the same basic pattern: Large islands have more species than small islands.

Figure 17.19 Species–Area Curves for Islands and Island-Like Habitats

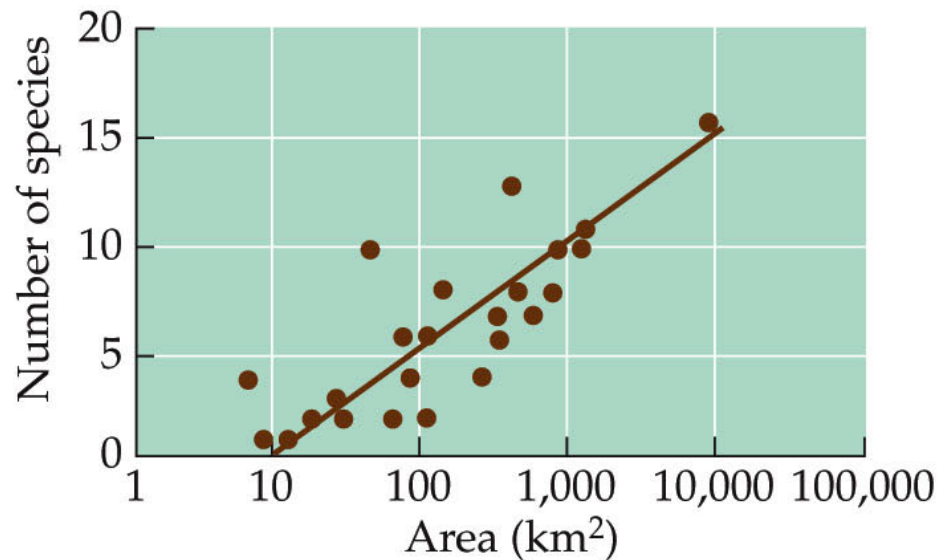
(A) Reptiles



(C) Fishes



(B) Mammals



Species diversity on islands also shows a strong negative relationship to distance from a source of species (e.g., the mainland or unfragmented habitat).

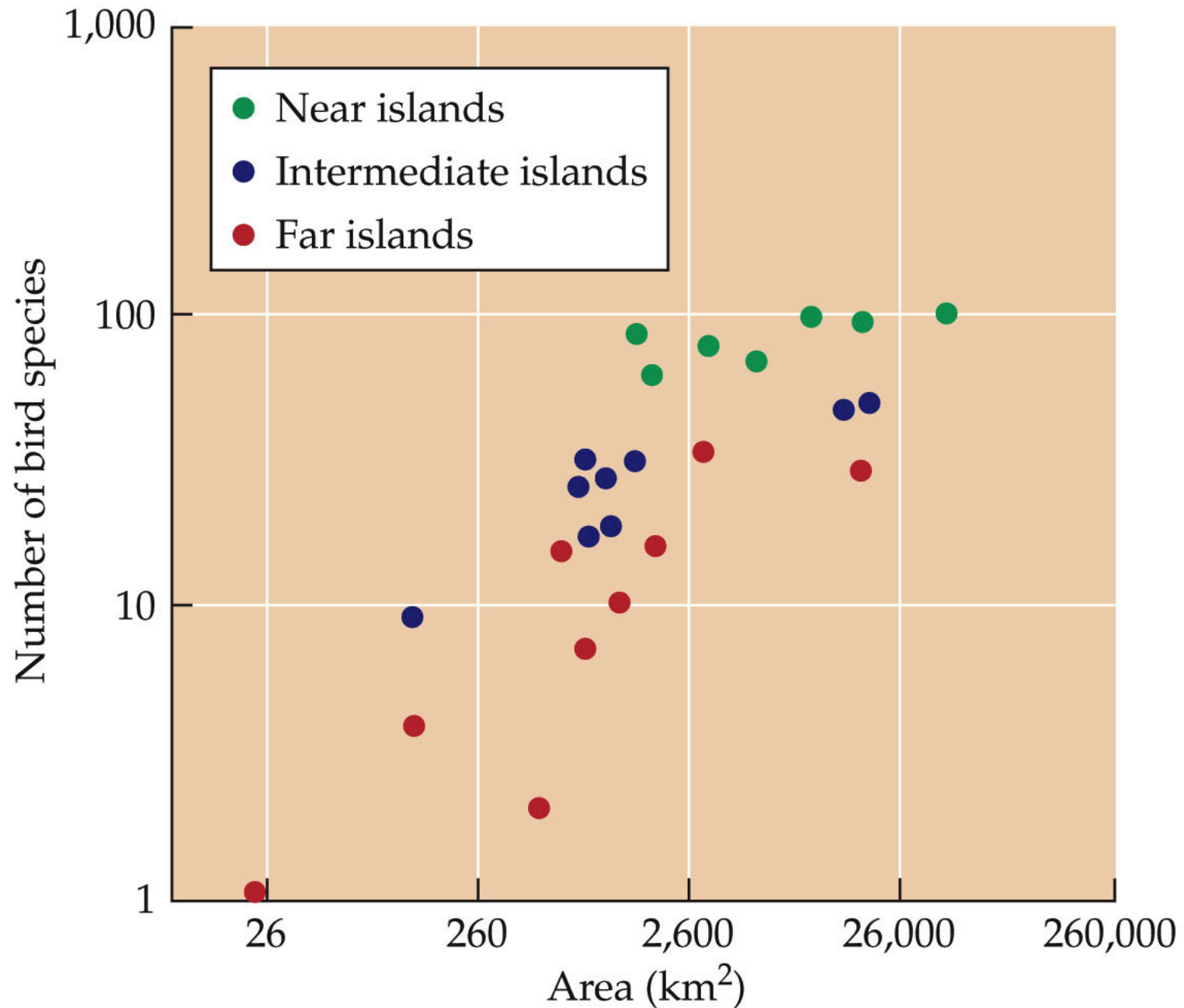
Island size and degree of geographic isolation are always confounded.

Regional Biogeography

MacArthur and Wilson (1963) plotted bird species richness and island area for a group of islands off New Guinea.

Islands of equal size had more species if they were closer to New Guinea.

Figure 17.20 Area and Isolation Influence Species Richness on Islands



Wilson, who studies ants, had made several observations about islands in the South Pacific:

- For every tenfold increase in island area, there was a doubling of ant species number.
- As ant species spread from mainland to islands, new species replaced existing species, but there was no net gain in species richness.

Regional Biogeography

There appeared to be an equilibrium number of ant species on the islands, which was dependent on their size and distance from the mainland.

But species composition on the islands could, and did, change over time.

MacArthur and Wilson developed these observations into a theoretical model, the **equilibrium theory of island biogeography**.

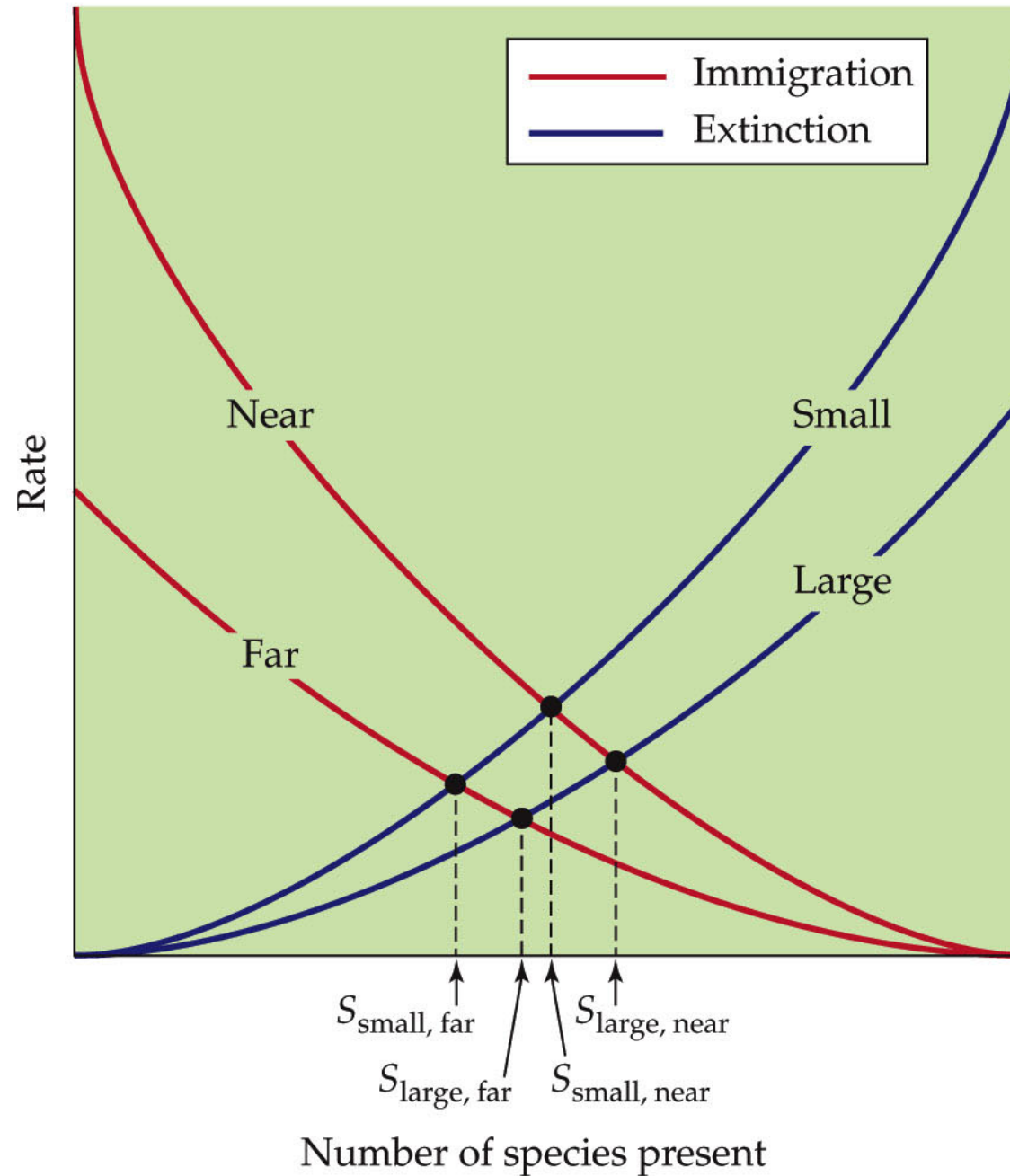
The number of species on an island depends on a balance between immigration rates and extinction rates.

Regional Biogeography

If immigration and extinction rates are plotted, the actual number of species on the island should fall where the two curves intersect.

This equilibrium number is the number of species that should theoretically “fit” on the island, irrespective of the **turnover**, or replacement of one species with another.

Figure 17.21 The Equilibrium Theory of Island Biogeography



They assumed that island size mainly controls extinction rates.

Populations on small islands have higher chances of going extinct, due to small population size, and increased effects of competition and predation.

Regional Biogeography

They assumed that distance from the mainland controls immigration rates.

Distant islands should have a lower immigration rate than near islands.

Regional Biogeography

MacArthur and Wilson applied their theory to data from the volcanic island of Krakatau.

The volcano erupted in 1883, wiping out all life. Scientists began observing the return of species within a year.

Data from three surveys of the island were available.

They calculated immigration and extinction rates of bird species and predicted that the island should sustain about 30 species at equilibrium, with a turnover of 1 species.

Bird species richness did reach 30 species within 40 years; and remained close to that number thereafter.

Figure 17.22 The Krakatau Test (Part 1)

(A)

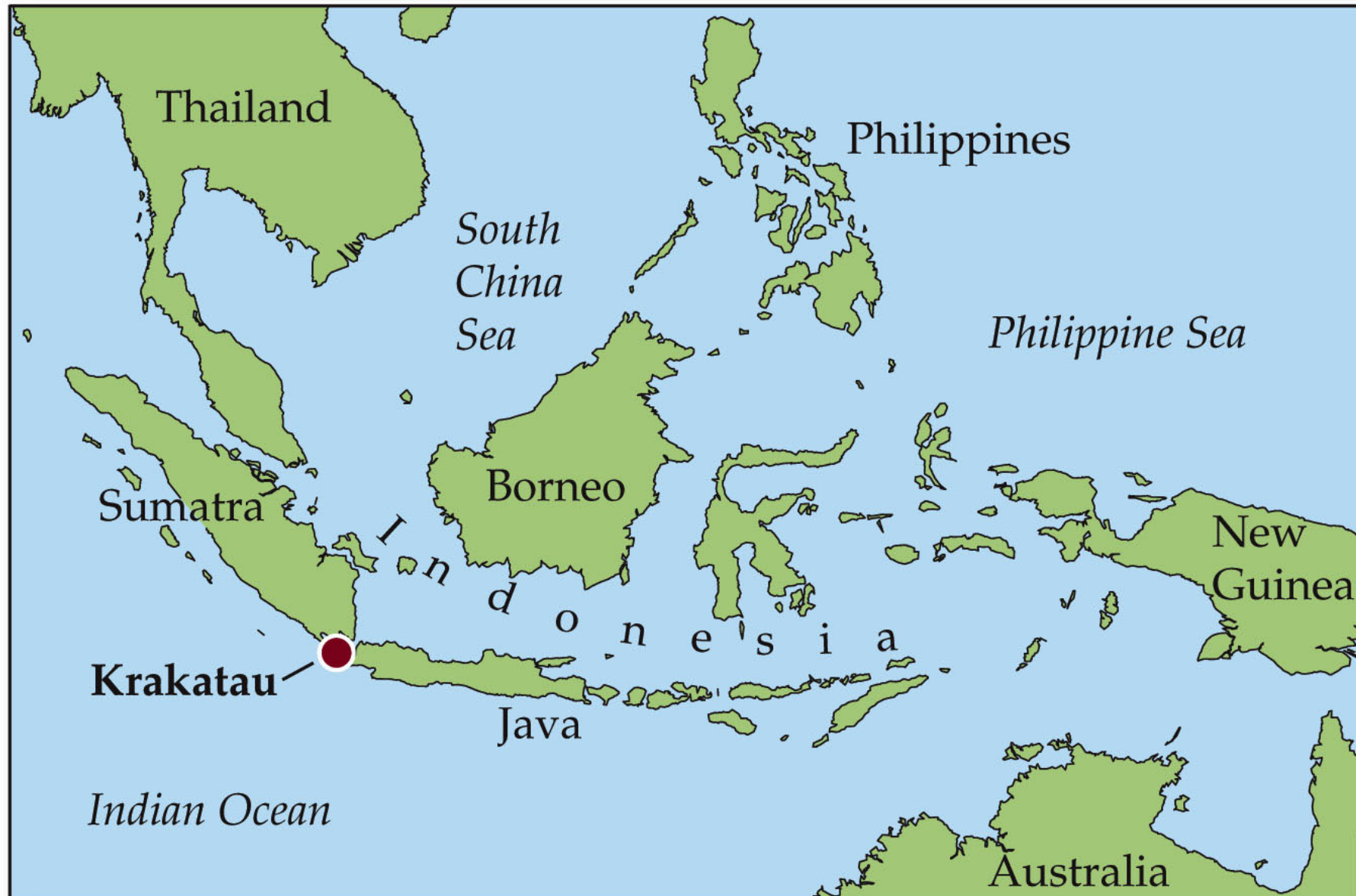
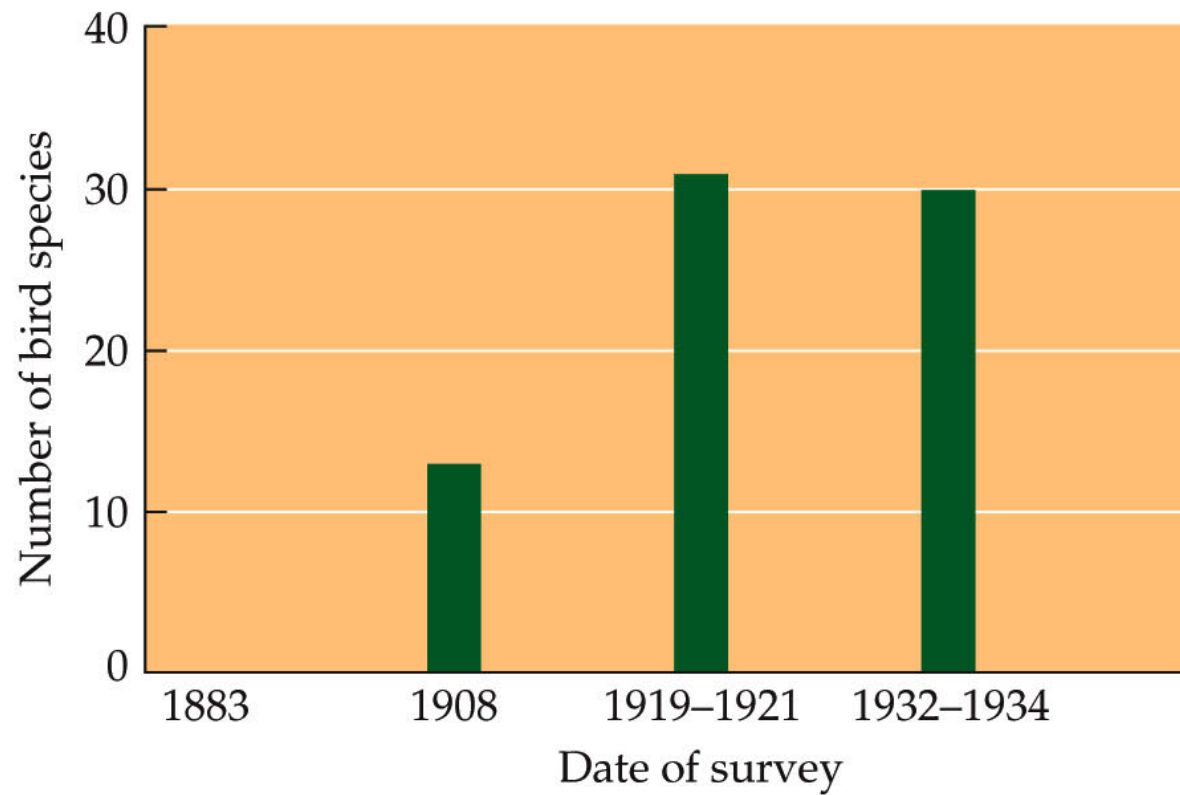
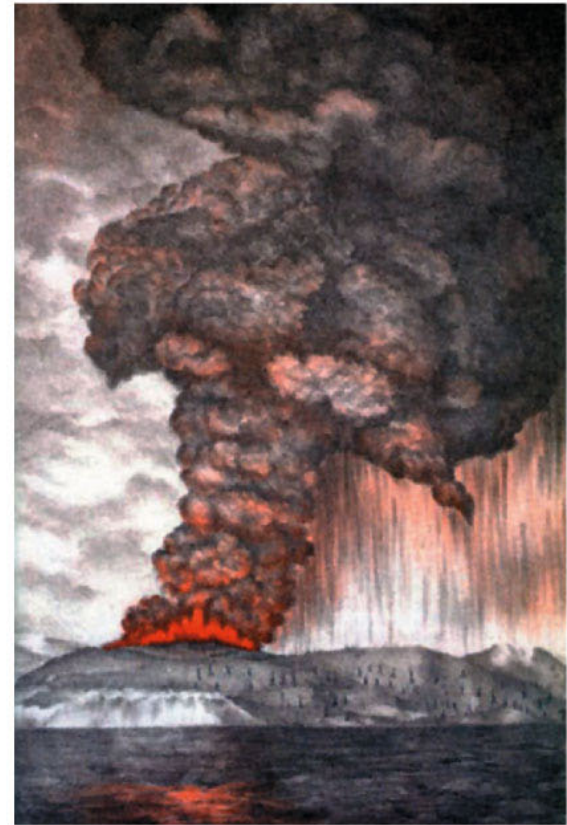


Figure 17.22 The Krakatau Test (Part 2)

(C)



(B)



But species turnover was about 5. This discrepancy motivated more research and manipulative experiments.

Simberloff and Wilson worked with mangrove islands in Florida, where they were able to manipulate whole islands.

Islands were sprayed with insecticides to remove all insects and spiders.

Regional Biogeography

After one year, species numbers were similar to numbers found before the experiment.

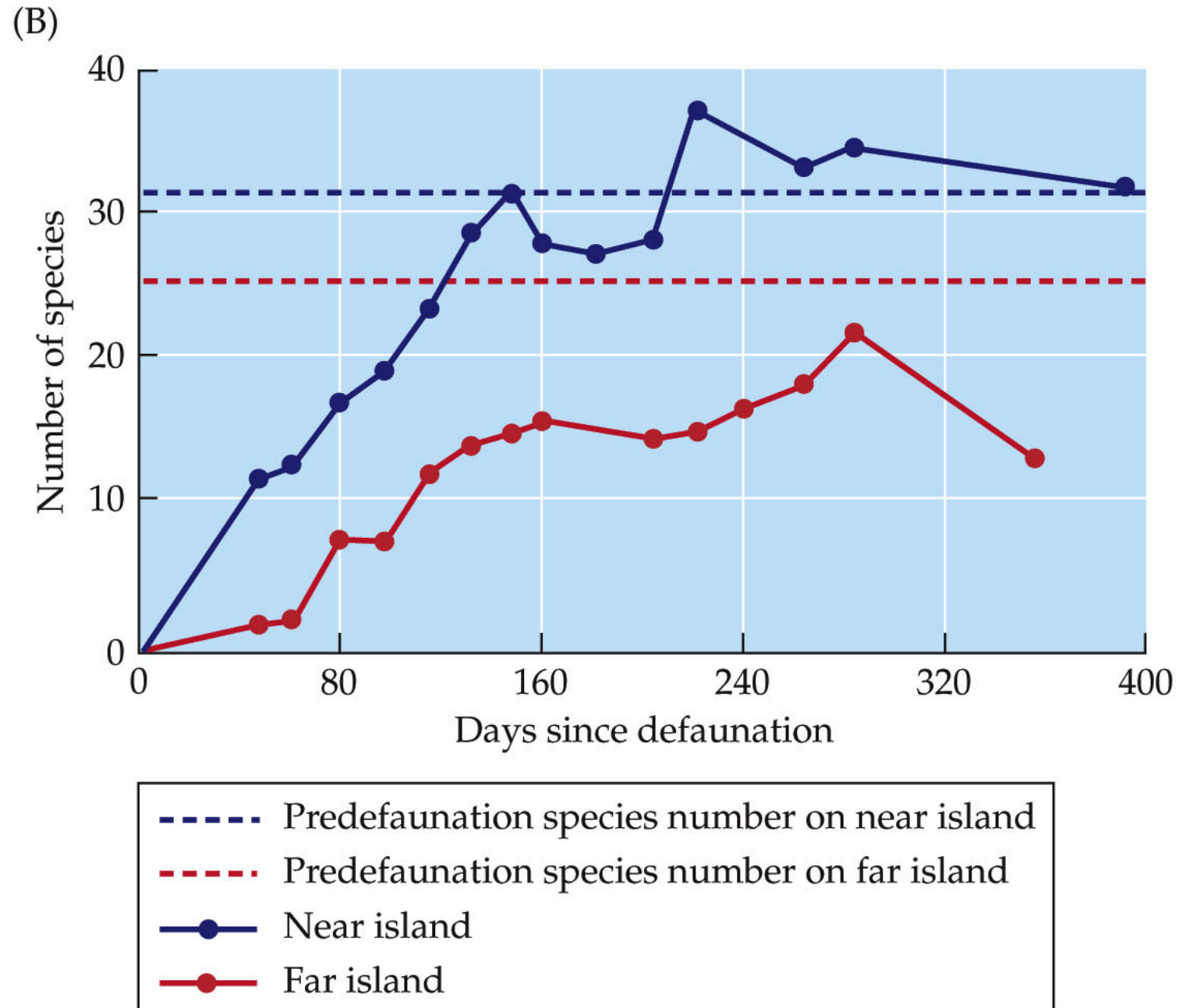
Also, islands closest to a source of colonists had the most species, and the farthest island had the least.

Figure 17.23 The Mangrove Experiment (Part 1)

(A)



Figure 17.23 The Mangrove Experiment (Part 2)



Regional Biogeography

How does the biogeography of mainland areas differ from islands?

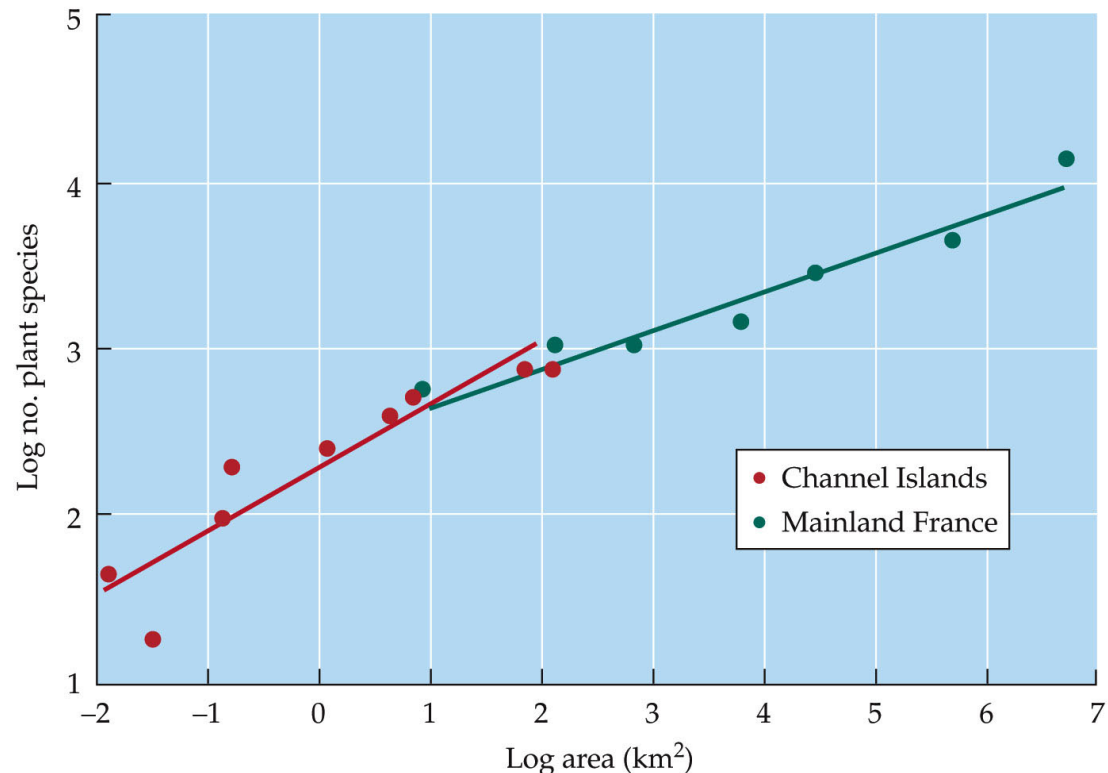
Mainland areas have very different rates of immigration and extinction.

Immigration rates are greater because there are fewer barriers to dispersal. Extinction rates are also lower because of continual immigration.

Regional Biogeography

Species on mainlands will always have a good chance of being “rescued” from local extinction by other population members.

The result is a less steep slope for species–area curves on mainlands.



Case Study Revisited: The Largest Ecological Experiment on Earth

One of the goals of the Biological Dynamics of Forest Fragments Project (BDFFP) was to study the effects of reserve design on the maintenance of species diversity.

They learned that habitat fragmentation had more negative and complicated effects than originally anticipated.

Case Study Revisited: The Largest Ecological Experiment on Earth

To maintain original species diversity, the forest fragments needed to be large and close together.

A survey of understory birds found that even the largest fragments (100 hectares) lost 50% of their species within 15 years (Ferraz et al. 2003).

Case Study Revisited: The Largest Ecological Experiment on Earth

Regeneration time for the rain forest is from several decades to a century.

So for forest islands (fragments) there would be no surrounding populations to “rescue” populations in the fragments.

Case Study Revisited: The Largest Ecological Experiment on Earth

They calculated that over 1,000 hectares would be needed to maintain bird species richness until forests could be regenerated—much larger than most existing fragments.

If forests were not regenerated, 10,000 hectares or more would be needed to maintain most of its bird species.

Case Study Revisited: The Largest Ecological Experiment on Earth

Even short distances between fragments hindered colonization.

Mammals, insects, birds, and others would not enter cleared spaces.

These organisms evolved in large, continuous, and climatically stable habitats.

Case Study Revisited: The Largest Ecological Experiment on Earth

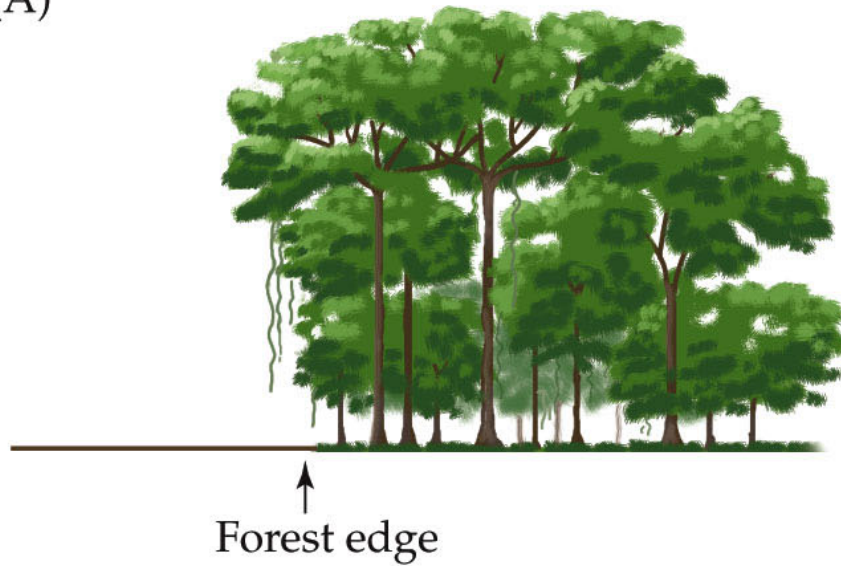
Habitat fragmentation also creates large **edge effects** at the transition between forest and nonforested habitat.

For example, trees at the edge are exposed to more light, higher temperatures, wind, fire, and diseases.

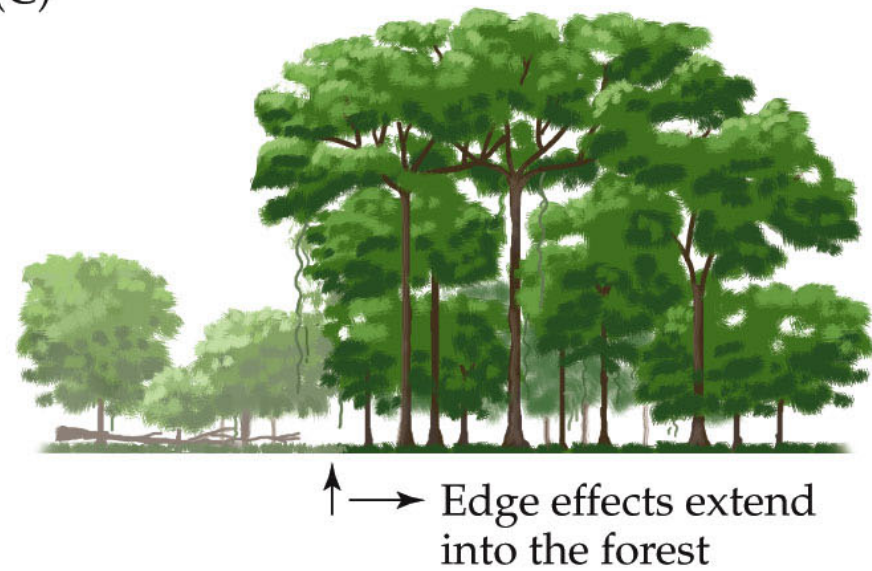
Edge effects can contribute to local extinctions.

Figure 17.24 Tropical Rainforests on the Edge

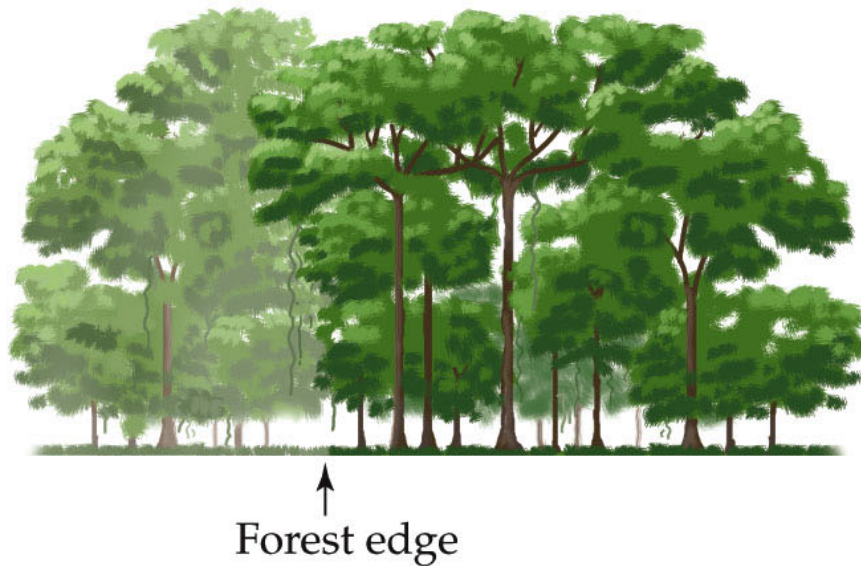
(A)



(C)



(B)



Case Study Revisited: The Largest Ecological Experiment on Earth

If the forest regenerates, secondary succession takes place and edge effects decrease.

If not, the area subjected to edge effects may increase in size.

Case Study Revisited: The Largest Ecological Experiment on Earth

In the southern Amazon, forest fragments are embedded in huge non-native sugarcane and *Eucalyptus* plantations.

Burning is used regularly, and keeps the forest edges in a constant state of disturbance.

Case Study Revisited: The Largest Ecological Experiment on Earth

Fire-tolerant plant species (many non-native) become more common in the edges, and become conduits for more fires.

This sets up a positive feedback loop that decreases the effective size of the forest fragment.

Some edge habitats can extend a kilometer or more into a fragment.

Case Study Revisited: The Largest Ecological Experiment on Earth

Research at the BDFFP has shown us that most forest fragments are too small to maintain all their original species.

Conservation will be most effective if we err on the side of larger, closer, and more numerous fragments.

Connections in Nature: Human Benefits of Tropical Rainforest Diversity

There are many reasons for concern over loss of tropical forest species, including ethical and aesthetic concerns.

There are also economic losses, such as those from timber harvesting.

80% of our diet originated in the tropics:
Corn, rice, potatoes, squash, yams,
oranges, coconuts, lemons, tomatoes,
and nuts and spices.

Connections in Nature: Human Benefits of Tropical Rainforest Diversity

25% of all commercial pharmaceuticals are derived from tropical rainforest plants, but less than 1% of tropical rainforest plants have been tested for their potential uses.

Connections in Nature: Human Benefits of Tropical Rainforest Diversity

In Cambodia, a study compared the total economic value of traditional forest uses (fuelwood, rattan and bamboo, malva nuts, and medicines) with the value of unsustainable forest harvesting.

The value of traditional forest uses is 4–5 times greater (\$700–\$3,900 per ha) than unsustainable forest harvesting (\$150–\$1,100 per ha).

Connections in Nature: Human Benefits of Tropical Rainforest Diversity

Until recently, we have not formally recognized the economic value of services provided by species or whole communities.

Tropical rainforests provide food, medicine, fuel, tourist destinations. They also regulate water flow, climate, and atmospheric CO₂ concentrations.

Connections in Nature: Human Benefits of Tropical Rainforest Diversity

Assigning economic value to these things is difficult.

It is easier to justify the use of rainforest timber and land for private profit than the conservation of rainforests for the ecological services that benefit society in general.

Private landowners must be given incentives to value the larger social benefits of ecological services.