

Island Biogeography

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A massive volcanic explosion in 1883 on the island of Krakatau in Indonesia destroyed two-thirds of the island, originally 11 km long and covered in tropical rain forest. Life on the remainder, an island known as Rakata, and the two neighboring islands, Panjang and Sertung, was eradicated, suffocated by tens of meters of volcanic ash. Recolonization on these islands has been studied by a series of scientists. Nine months after the 1883 eruption, the first reported colonist of Rakata was a spider spinning its web. Plant colonization of Rakata was greatly affected by how well plants were able to disperse. Wind- or sea-dispersed plants were able to colonize the island much more readily than plants dispersed by animals, such as birds (**Figure 21.1**). The early plant community was dominated largely by grasses. By 1929, over 40 years after the original eruption, animal-dispersed plants became as common as sea-dispersed ones, probably because the birds had become more abundant on the island. In 1930 a submarine eruption produced a fourth island, Anak Krakatau.

In Chapter 20, we explored the phenomenon called succession, the gradual and continuous change in species composition and community structure over time following a disturbance. On islands especially, succession is affected by the distance that dispersing organisms have to travel from undisturbed mainland areas. If a source pool of potential dispersing species is close by, then succession occurs quite rapidly. If there are long distances separating potential new colonists from areas to be recolonized, then succession may be slower and some species may never colonize. Also, if an island to be recolonized is large it may accrue more species than smaller areas. In this chapter we investigate how the size of the area of habitat to be colonized, and the distance of the source pool of colonists affect the special case of succession on islands. We also examine species turnover where certain immigrants to islands may be replaced by other species over time.

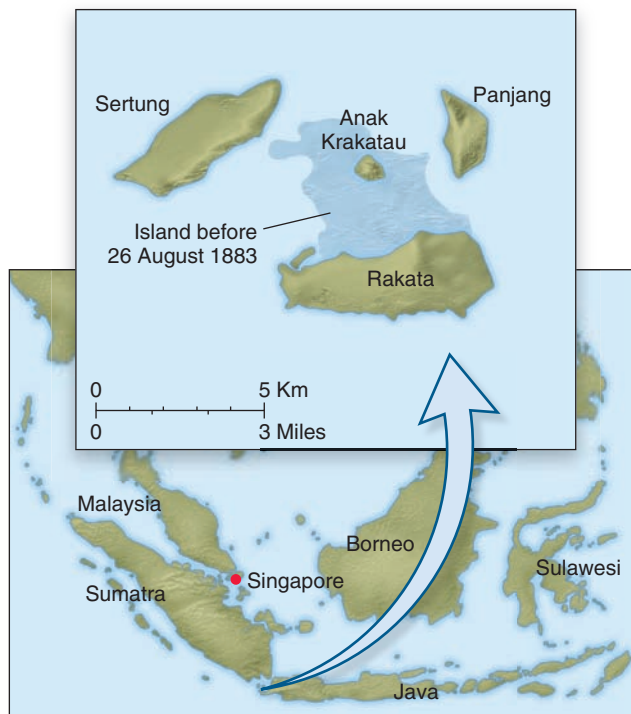
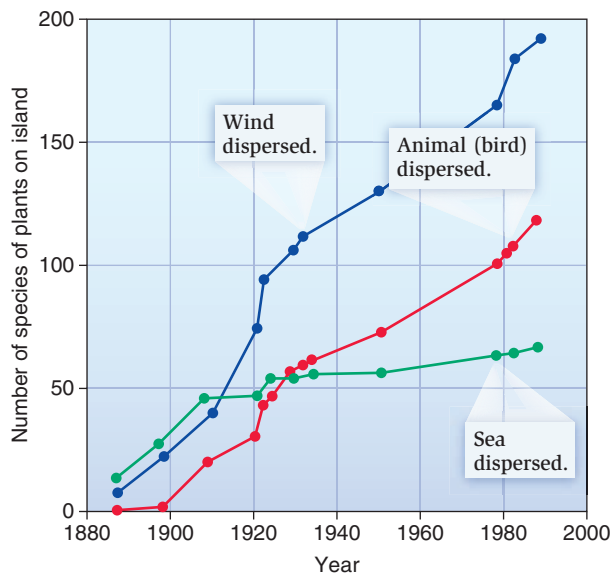


Figure 21.1 Plant colonization on Rakata following volcanic eruption. Initially wind- and sea-dispersed plants, especially grasses, dominated the flora. (From data in Whittaker, et al., 1992.)

21.1 The Theory of Island Biogeography Considers Succession on Islands

Robert MacArthur and E. O. Wilson (1963, 1967) developed a comprehensive model to explain the process of succession on newly formed islands, where a gradual buildup of species proceeds from a sterile beginning. Their ideas are termed the **theory of island biogeography**. In this section, we explore island biogeography and how well the theory's predictions

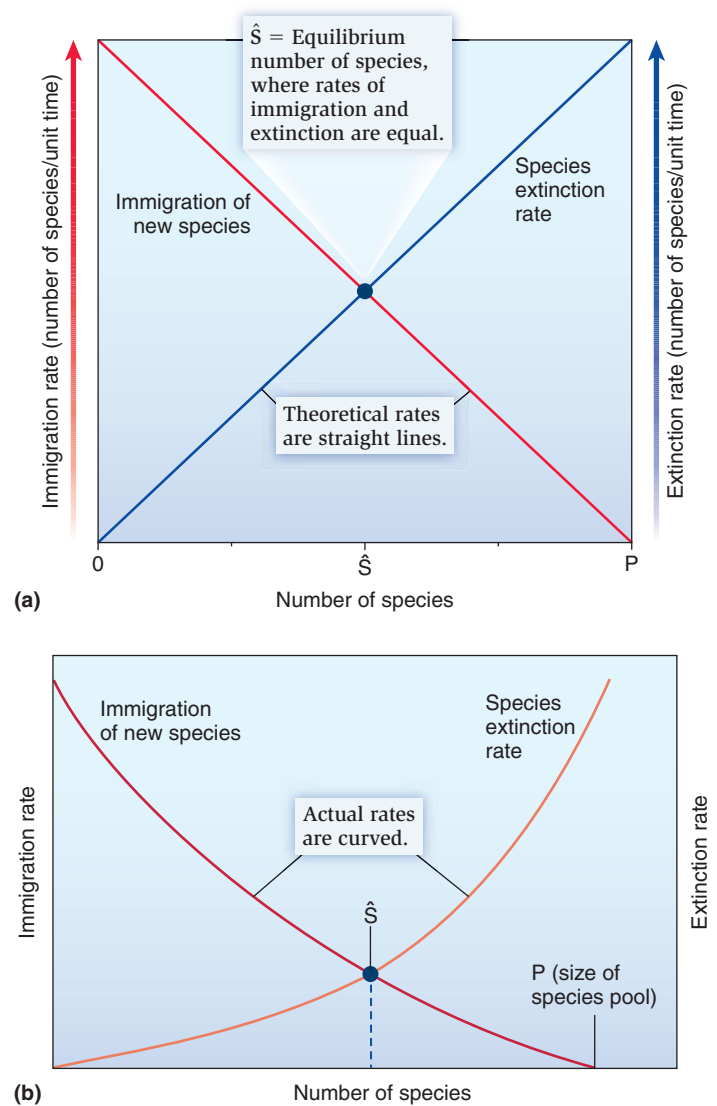


Figure 21.2 The theory of island biogeography.

(a) The interaction of immigration rate and extinction rate produces an equilibrium number of species on an island, \hat{S} . \hat{S} varies from 0 species to P species, the total number in the species pool of colonists. (b) In practice, the rate curves bend because some species immigrate more readily than others and because some species are better competitors than others.

are supported by data, particularly that provided by classic experiments in the Florida Keys.

MacArthur and Wilson's theory of island biogeography suggests that species repeatedly arrive on an island and either thrive or become extinct. The number of species tends toward an equilibrium number that reflects a balance between the rate of immigration and the rate of extinction (**Figure 21.2a**). The rate of immigration of new species is highest when no species are present on the island, so that each species that invades the island is a new species. As species accumulate, subsequent immigrants no longer represent new species. The rate of extinction is low at the time of first colonization,

because few species are present and most have large population sizes. With the addition of new species, the population sizes of some species may happen to be smaller, so the probability of extinction of these species by chance alone increases. Species may continue to arrive and go extinct, but the number of species on the island remains the same.

MacArthur and Wilson reasoned that when plotted graphically, both the immigration and extinction lines would be curved for several reasons (**Figure 21.2b**). First, species arrive on islands at different rates. Some organisms, including plants with seed-dispersal mechanisms and winged animals, are more mobile than others and will arrive quickly. Other organisms will arrive more slowly. This pattern causes the immigration curve to start off steep but get progressively shallower. On the other hand, extinctions start off slowly and rise at accelerating rates, because as later species arrive, competition increases and more species are likely to go extinct. Earlier arriving species tend to be *r*-selected species, which are better dispersers, whereas later arriving species are generally *K*-selected species, which are better competitors. Later arriving species usually outcompete earlier arriving ones, causing an increase in extinctions.

Since MacArthur and Wilson's work, their concept of island biogeography has been applied to mainland areas, where patches of particular habitat can be viewed as "islands" in a sea of other, unsuitable habitat. Thus, patches of grassland in the Craters of the Moon National Monument in Idaho are surrounded by extensive lava flows (**Figure 21.3**). For the animals that inhabit the grassland, the lava flows may as well be a real ocean because the animals cannot survive in these inhospitable areas. Similarly, freshwater species that live in lakes behave as if they were in islands surrounded by a "sea" of dry land.

Dan Janzen (1968) extended the habitats-as-islands concept by proposing that individual host-plant species could be islands to their associated herbivore fauna, which was adapted only to feed on that particular type of vegetation. For example, many insects have sophisticated biochemical machinery that allows them to detoxify certain plant tissues. However, the machinery is so specialized that it will only work for one or two species of host plant. All other plants are essentially inedible to the insect. An example is the monarch butterfly caterpillar, which can feed only on milkweed plants. For the monarchs, milkweed patches are effectively islands surrounded by other vegetation that might as well be open ocean.

The strength of the island biogeography model was that it generated several falsifiable predictions:

1. The number of species should increase with increasing island size. This is also known as the **species-area hypothesis**. Extinction rates would be less on larger islands because population sizes would be larger and less susceptible to extinction (**Figure 21.4**).
2. The number of species should decrease with increasing distance of the island from the mainland, or the **source**



Figure 21.3 Habitat islands. Idaho's Craters of the Moon National Monument contains patches of grassland habitat surrounded by inhospitable lava.

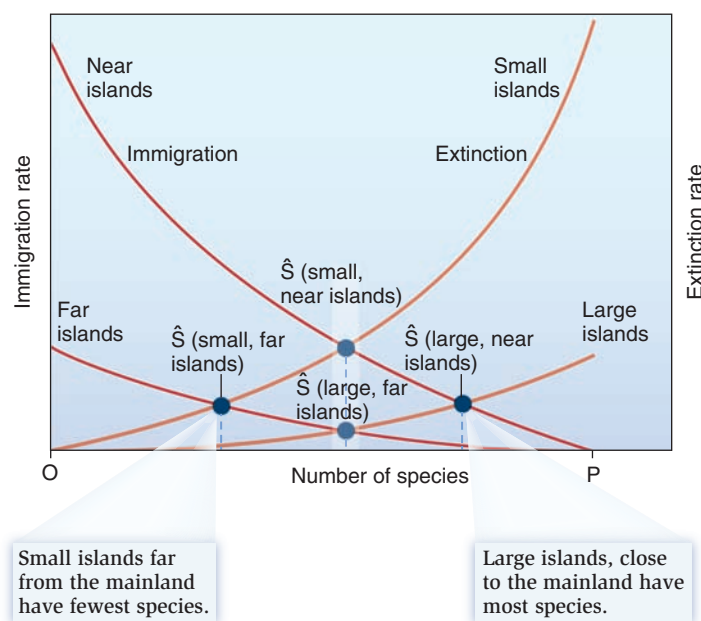


Figure 21.4 Island biota size varies with distance from the source pool and island size. An increase in distance, from near to far, lowers the immigration rate; an increase in island area, from small to large, lowers the extinction rate. The intersection of the immigration and extinction curves yields the equilibrium number of species. (After MacArthur and Wilson, 1963.)

pool, the pool of species that is available to colonize the island. Immigration rates would be greater on islands near the source pool because species do not have as far to travel (**Figure 21.4**). This is also known as the **species-distance hypothesis**.

3. The number of species on an island might remain the same, but the composition of the species should change

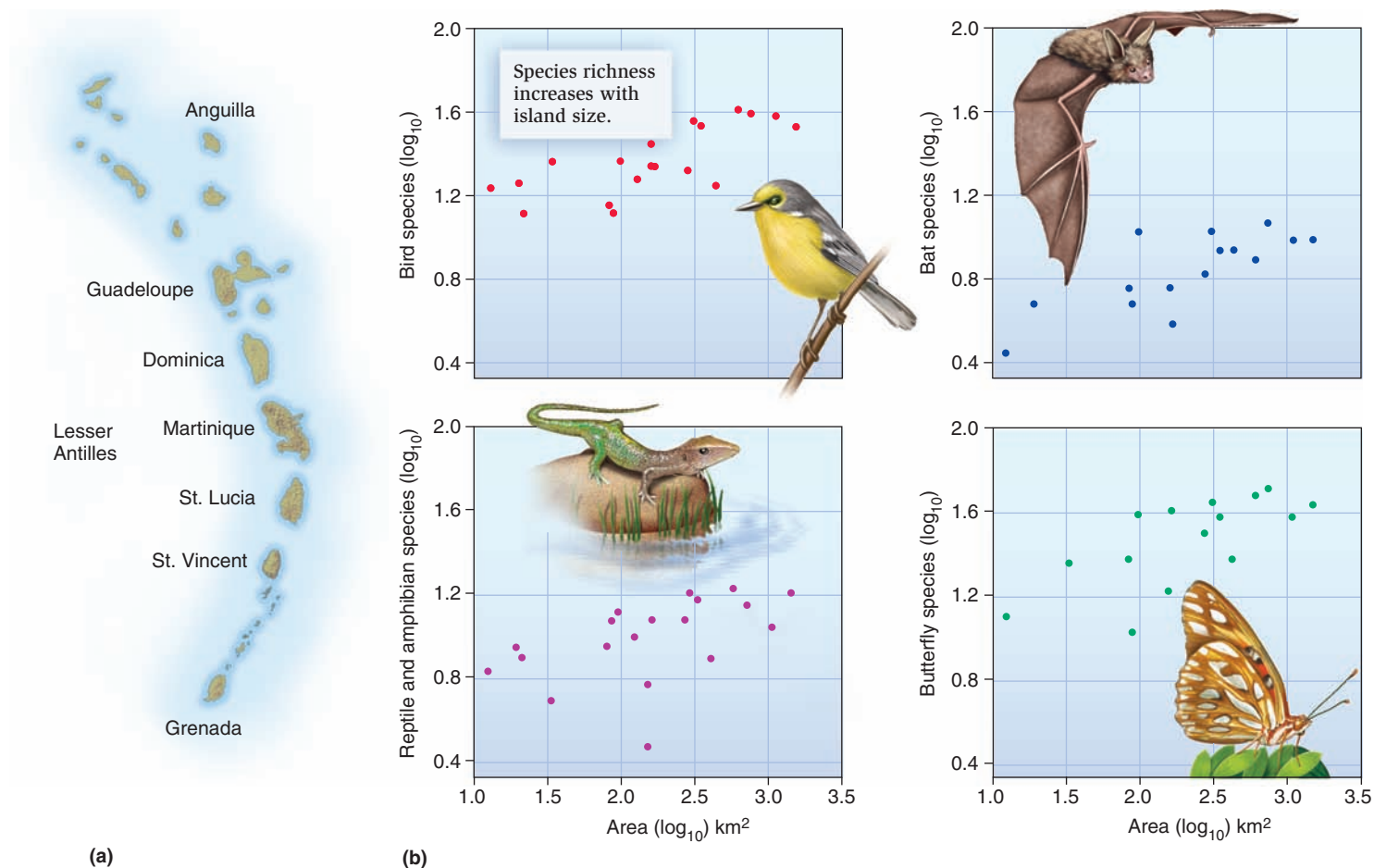


Figure 21.5 Species richness increases with island size. (a) The Lesser Antilles extend from Anguilla in the north to Grenada in the south. (b) The number of reptile and amphibian, bird, butterfly, and bat species increases with the area of an island.

ECOLOGICAL INQUIRY

Approximately how large is the change in bird species richness across islands in the Lesser Antilles?

continuously as new species colonize the island and others become extinct. The turnover of species should therefore be considerable.

Let's examine these predictions one by one and see how well the data support them.

21.1.1 The species-area hypothesis describes the effect of island size on species richness

The West Indies has traditionally been a key location for ecologists studying island biogeography. This is because the physical geography and the plant and animal life of the islands are well known. Furthermore, the Lesser Antilles, from Anguilla in the north to Grenada in the south, enjoy a similar climate and are surrounded by deep water (**Figure 21.5a**). Robert Ricklefs and Irby Lovette (1999) summarized

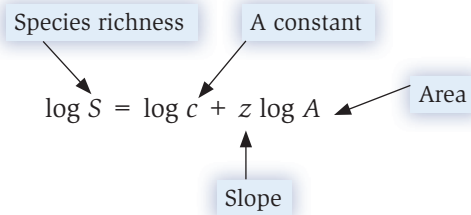
the available data on the species richness of four groups of animals, birds, bats, reptiles and amphibians, and butterflies, on over 19 islands that varied in area over two orders of magnitude, 13–1,510 km². In each case, there was a significant relationship between area and species richness (**Figure 21.5b**). As area increased, so did species richness.

Note that these relationships are traditionally plotted on a double logarithmic scale, a so-called log-log plot, in which the horizontal axis is the logarithm to the base 10 of the area and the vertical axis is the logarithm to the base 10 of the number of species. A linear plot of the area versus the number of species would be difficult to produce, because of the wide range of area and richness of species involved. Logarithmic scales condense this variation to manageable limits and also produce a linear relationship instead of a curvilinear one.

We can represent the relationship of species richness to area with the equation:

$$S = cA^z$$

or in logarithmic form,



where S = number of species, and c and z are both constants.

In this relationship, z values are often taken to represent the slope of the relationship between species richness and area. One of the early topics of discussion in island biogeography was the significance of variations in the value of z . A high value of z indicates steep increases in species number as island size increases, whereas low values indicate much smaller differences in numbers of species between islands. Values of z obtained from habitat islands, patches of suitable habitat on mainland areas, often vary from 0.15 to 0.25, lower than those from truly insular situations, where z is often 0.20 to 0.40. This means that as larger areas are sampled, fewer new species are added on habitat islands than on true islands. The biological explanation for this phenomenon is that habitat islands contain some transient species from adjacent habitats, because on habitat islands, some species are simply resting while passing through an area. There are proportionately more transients passing through smaller areas, raising the apparent number of species in those areas, so the slope of the species-area curve is shallow for habitat islands. Islands, by contrast, are actual isolates with reduced migration rates, because species cannot rest up in the ocean between the islands, so the number of transients on a true island is reduced. Differences in z values may also result from differences in dispersal ability of different taxa.

Jim Brown (1978) studied the distribution of forest-dwelling mammals and birds on mountaintops in the isolated ranges of Nevada's Great Basin National Park. The mountain ranges are essentially isolated from one another, and the mammalian fauna is a relict community of a bygone age when rainfall was higher and this type of forest habitat was contiguous. Each mountaintop is a "sky island," essentially a forest remnant atop a mountain in a sea of desert (Figure 21.6a).

Brown found a significant relationship between species richness and area for both birds and mammals. The species-area relationship for birds on Brown's mountaintops (Figure 21.6b) had a slope of 0.165; that for mammals, 0.326 (Figure 21.6c). The slope of the line for mammals was thus more like that found on true islands. The reason is that there is little mammalian migration between mountaintops because mammals would have to walk down the mountain, across the valley, and up the next mountain. In this situation, "sky islands" behave more like true islands. In contrast, birds

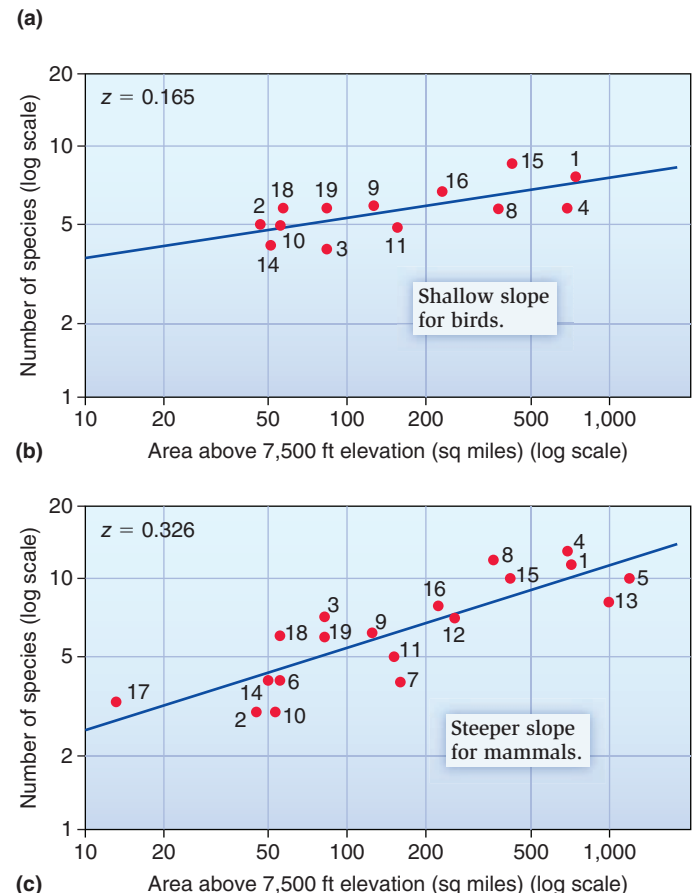
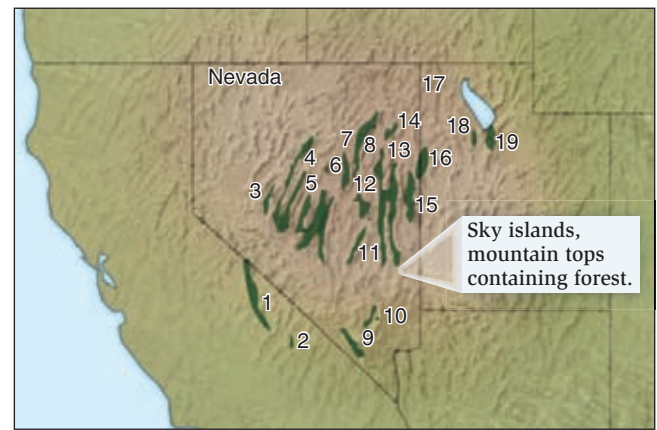


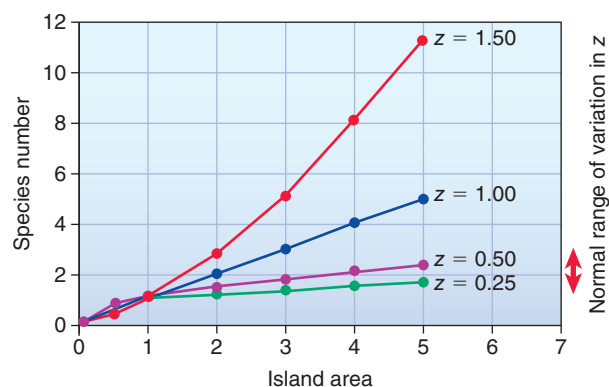
Figure 21.6 The equilibrium theory of island biogeography applied to "sky islands." (a) Map of the Great Basin region of the western United States showing the isolated mountain ranges between the Rocky Mountains on the east and the Sierra Nevada on the west. (b) The species-area relationship for the resident boreal birds of the mountaintops in the Great Basin shows a shallow slope. (c) The species-area relationship for the boreal mammal species shows a steeper slope. Numbers refer to sample areas on the map. (After Brown, 1978.)

ECOLOGICAL INQUIRY

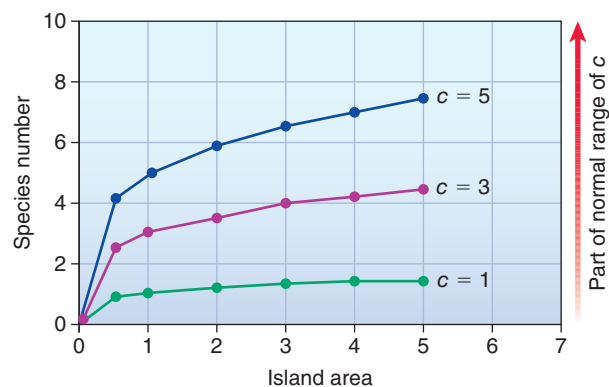
Why is the slope of the line steeper for mammals than for birds?

disperse more readily than mammals because they can fly between mountaintops, and the z value in their case is more consistent with other habitat islands.

The constant c is often thought of as the number of species per unit area, for example, per hectare of forest or grassland. It is affected by many factors and is likely to be higher for productive habitats. Tropical islands have greater c values than temperate ones. For example, islands of the Malayan Archipelago, a tropical location, and of the Shetland Islands, off the coast of Scotland, both have z values of 0.31 for land birds. However, the c value for Malayan Islands is 10.19 and for the Shetland Islands 6.90, indicating the Malayan Islands have 1.48 times as many bird species as Shetland Islands of the same area. This is not surprising given the tropical forest of Malaya is rich in species as compared to the more scantily vegetated Scottish islands. Distance to a rich source pool also affects c . A series of islands close to the mainland would have many species and a high c value. A series of distant islands of the same size would have fewer species per unit area. Finally, c is affected by the taxon of interest. It is likely to be higher for invertebrates than vertebrates, because there are many more species of invertebrates per unit area than there are of vertebrates.



(a) c held constant



(b) z held constant

Figure 21.7 The effects of varying values of c and z on the species-area relationship (a) Effects of varying z ; c is held constant at 1. (b) Effects of varying c ; z is held constant at 0.25. (After Lomolino, 1989.)

Mark Lomolino (1989) showed that variation in c values affected species-area relationships more than variation in z values. First, most z values vary little, typically between 0.15 and 0.35, which is not sufficient to change species number (**Figure 21.7a**). On the other hand, c values vary much more, from less than 4 to over 16. Such variation is sufficient to quite dramatically affect species number (**Figure 21.7b**).

Apart from Ricklefs and Lovette's and Brown's studies, species-area relationships exist for birds of the East Indies, beetles on West Indian islands, ants in Melanesia, and land plants of the Galápagos. In addition, a species-area relationship was demonstrated for the insects feeding on British trees (refer back to Figure 18.5) and for the insects feeding on bracken fern (**Figure 21.8**). This provides strong support for this prediction of the equilibrium model of island biogeography.

Experimental support for the effect of area on species richness was provided by Daniel Simberloff (1978), a student of E. O. Wilson who studied islands of pure mangroves in the Florida Keys. He painstakingly crawled on his hands and knees to collect every species that fed on the islands, which were mainly very small insect species. Simberloff then created his own reduced-area islands by taking a chain saw and felling trees to make the island smaller. The felled material was hauled

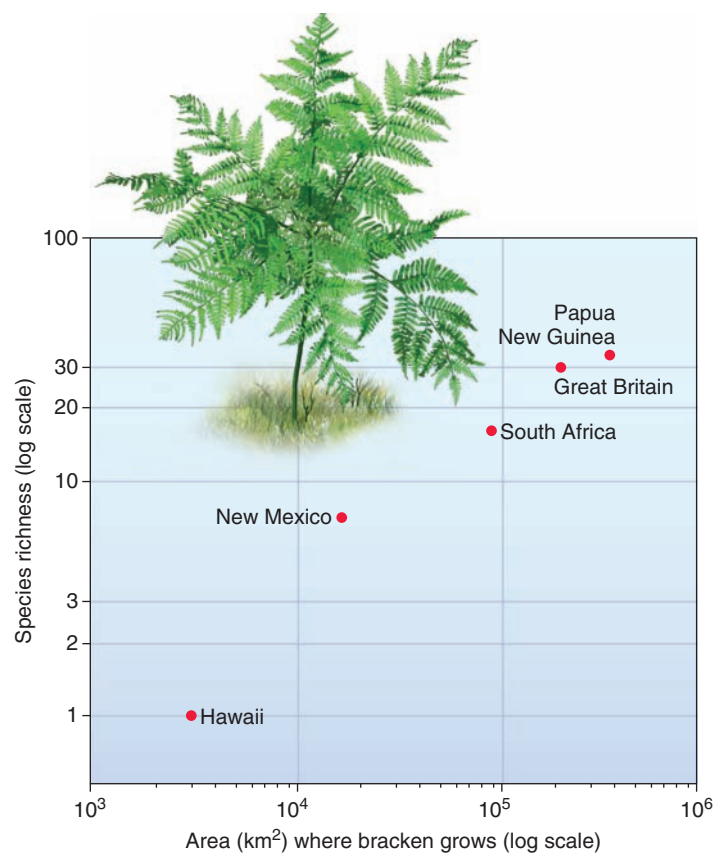


Figure 21.8 Species-area relationship. For the herbivores feeding on bracken fern in different areas of the world. (After Compton, et al., 1989.)

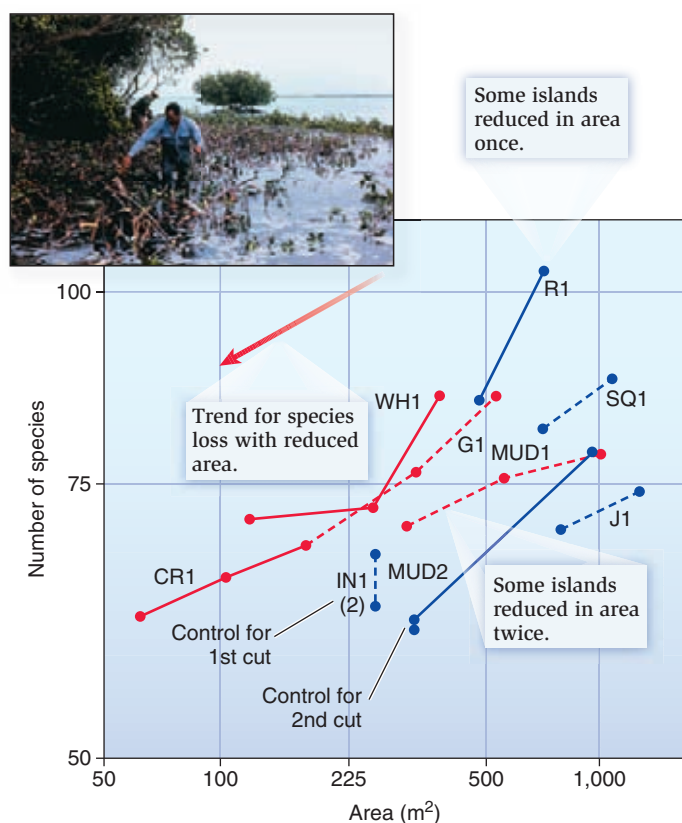


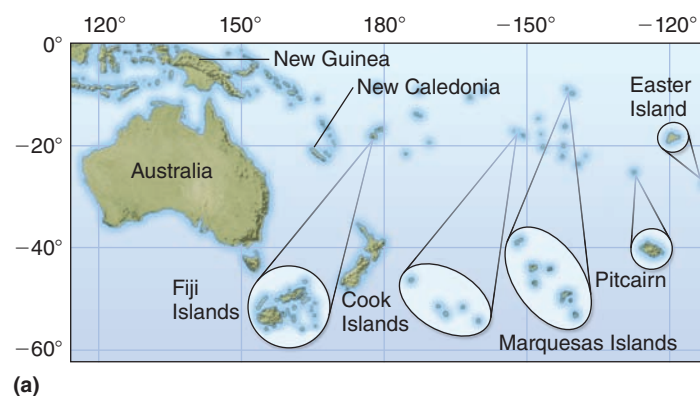
Figure 21.9 Reduction in species numbers on mangrove islands with area reduced by chain saw. Solid lines connect blue dots, representing where island area was experimentally reduced once. Red dots and dotted lines represent four islands where area was reduced twice. (After Simberloff, 1978.)

away in a barge. (One could probably not get a permit to do this experiment today, as mangroves now are legally protected.)

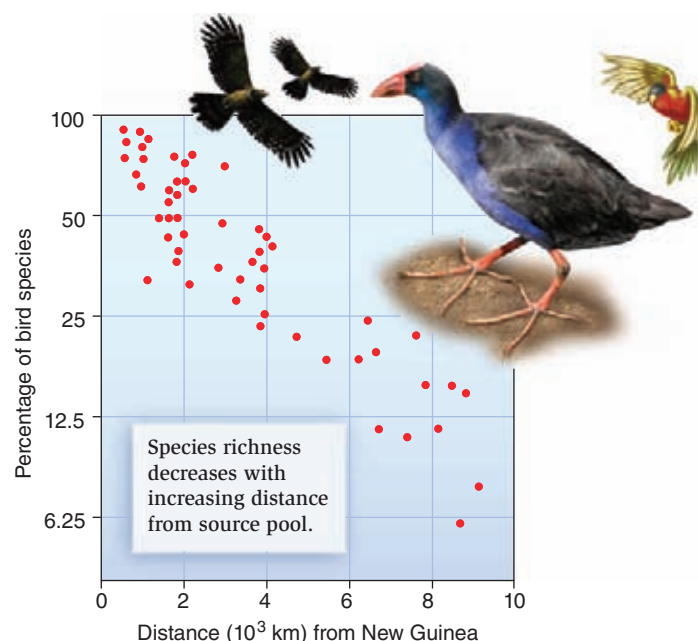
Simberloff reduced the area of eight islands and left one as a control (IN1). Seven months later, after enough time had passed for insects to become re-established following this disturbance, he censused again. Insect densities had dropped on all eight islands but increased slightly on the control (**Figure 21.9**). He then further reduced the areas of four of the islands (WH1, CR1, MUD1, and G1) and left one island (MUD2) as a control. A year later a final census was made, and species richness had again dropped on the four islands but not on MUD2. The results clearly indicated that area affects species number. Some ecologists have used the species-area relationship to predict species extinction rates as wildlife habitat continues to shrink due to the human activities of deforestation, agriculture, and urbanization (see **Global Insight**).

21.1.2 The species-distance hypothesis describes the effect of island distance on species richness

MacArthur and Wilson also marshaled evidence for the effect of the distance of an island from a source pool of colonists,



(a)



(b)

Figure 21.11 Species richness decreases with distance from the source pool. (a) Map of Australia, New Guinea, and these Polynesian Islands: New Caledonia, Fiji Islands, Cook Islands, Marquesas Islands, Pitcairn, and Easter Island. (b) The numbers of bird species on islands is observed to decrease with increasing distance from the source pool, New Guinea. Species richness is expressed as the percentage of that on New Guinea.

usually the mainland. In studies of the numbers of lowland forest bird species in Polynesia, they found that the number of species decreased with the distance from New Guinea, the source pool in this case (**Figure 21.11**). They expressed the richness of bird species on the islands as a percentage of the number of bird species found on New Guinea. There was a significant decline in this percentage with increasing distance, and more distant islands contained lower numbers of species than nearer islands. This research substantiated the prediction of species richness declining with increasing distance from the source pool.



Deforestation and the Loss of Species

If species richness on habitat islands increases with area, extinction should result as area declines. Just how many species are lost with habitat shrinkage is the critical question. To some extent, this depends on the value of z , the slope of the relationship between species richness and area. We can measure deforestation or habitat area lost fairly accurately given satellite images, but just how many species become extinct for each unit of habitat that is destroyed? We know that z values are commonly found to be between 0.15 and 0.35 for a variety of taxa, so we can use these types of values in the species-area relationship to estimate species loss (**Figure 21.10**). If $c = 10$ and $z = 0.2$, a 90% decrease in habitat area, from 1,000 to 100 hectares, would result in a 36.9% loss of species:

$$S = cA^z$$

$$S = 10 \times 1,000^{0.2}$$

$$S = 39.81$$

If the area is reduced by 90%:

$$S = 10 \times 100^{0.2}$$

$$S = 25.11$$

This is a loss of 14.7 species, or 36.9%.
If $z = 0.35$, then the loss would be 55%.

$$S = cA^z$$

$$S = 10 \times 1,000^{0.35}$$

$$S = 112.20$$

If the area is reduced by 90%:

$$S = 10 \times 100^{0.35}$$

Roger del Moral (2000) investigated the colonization by plants of four plots on Mount St. Helens following the eruption in 1980. Two “near” plots were less than 50 m from the intact forest and two “distant” plots were over 200 m distant. Species accumulated quicker on near plots than on distant plots (**Figure 21.12**). By the year 2000, the area covered by plants in the isolated plots was only 50% that of the near plots (**Figure 21.12b**). In part, this was because fruit-eating birds that disperse seed seldom disperse more than 50 m from the forest.

Finally, Manuel Nore's (1995) documented the number of bird species on montane forest islands on mountaintops near the Andes in Venezuela, Colombia, and Ecuador. The Andes

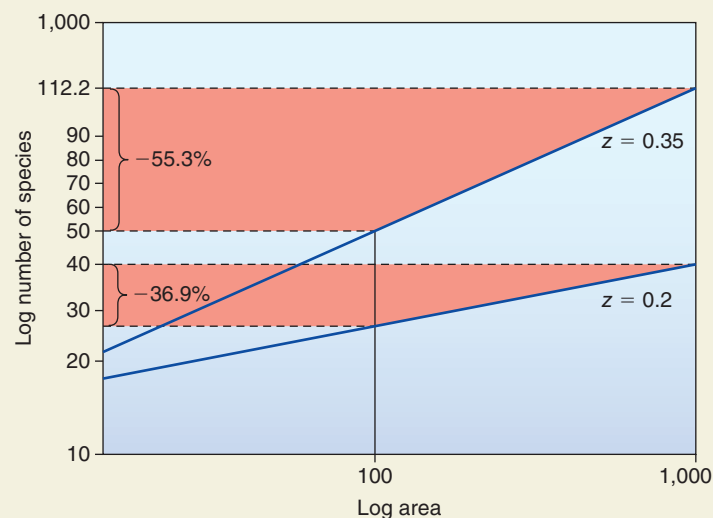


Figure 21.10 The effects of habitat loss on species abundance based on the species-area relationship, $S = cA^z$. Here $c = 10$ and $z = 0.2$ or 0.35 . Where $z = 0.35$, a 90% loss in habitat results in a 55% loss in species. Where $z = 0.2$, a 90% loss in habitat results in a 36.9% loss in species. (After Groom, et al., 2006.)

$$S = 50.11$$

This is a loss of 62.09 species, or 55%.

There are two conclusions from these examples. First, greater z values, steeper slopes, result in greater species lost as habitat is lost. Second, because of the logarithmic nature of the species-area relationship, a 90% loss in forest habitat doesn't translate into a 90% loss in species.

acted as the source pool of the birds, and species richness on these sky islands decreased the farther they were from the Andes (**Figure 21.13**).

21.1.3 Species turnover on islands is generally low

Studies involving species turnover on islands are difficult to perform because detailed and complete species lists are needed over long periods of time, usually many years, often decades, before and after disturbances. The lists that do exist, before disturbances, are often compiled in a casual way and are not usually suitable for comparison with more modern

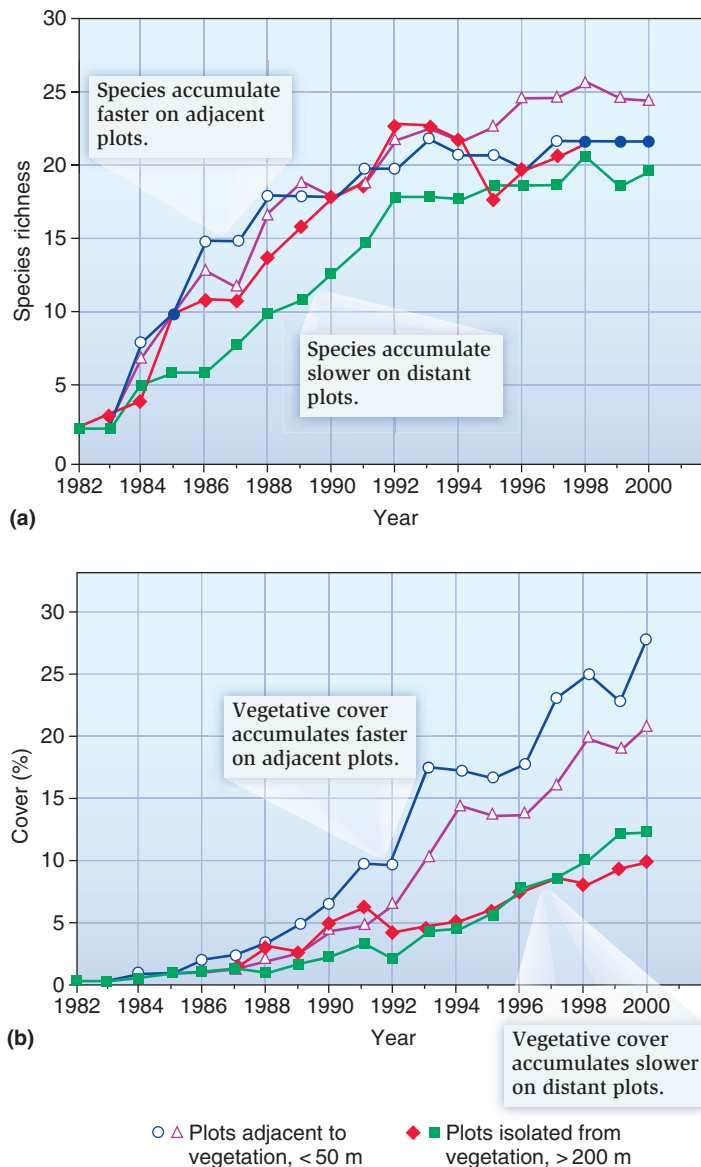


Figure 21.12 Effects of distance on recolonization on Mount St. Helens, following the eruption of 1980. (a) Species richness and (b) percent cover both recover faster on plots closer to intact vegetation (< 50 m) than plots that were more isolated (> 200 m). (After del Moral, 2000.)

data. For example, Jared Diamond (1969) studied the birds of the California Channel Islands in 1968 and compared his species lists to those of an earlier study published in 1917 by A. B. Howell. Diamond reported that many birds, about 5–10 species per island, reported from Howell's survey were no longer present but just as many species not reported by Howell had apparently colonized. The logic was that the species richness of islands was the same in 1969 as it was in 1917, but identities had changed, indicating species turnover. This was just what MacArthur and Wilson would predict.

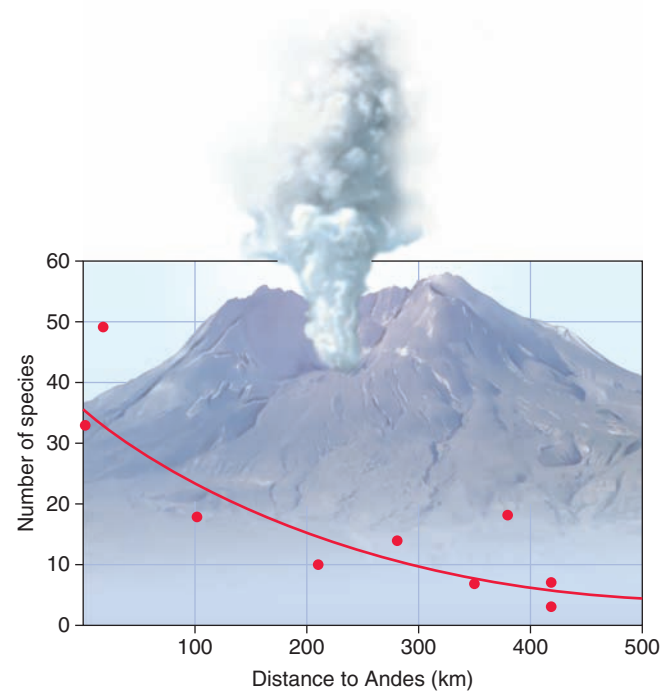


Figure 21.13 Species richness decline of montane forest birds with increasing distance from the Andes mountains. (After Nores, 1995.)

However, other authors were quick to point out that Howell's list was not exhaustive and was just a summary of all known breeding records, some from as far back as 1860–1870.

Diamond went on to carry out similar comparisons of bird species over time on islands near New Guinea, but once again the earlier surveys included no extensive field notes and Diamond was forced to compare his species richness lists of islands to collections of species made earlier. If a species had been seen but not collected, then the comparisons would be invalid. Francis Gilbert (1980) reviewed 25 investigations carried out to demonstrate turnover and found a lack of this type of rigor in nearly all of them. Furthermore, most of the observed turnover in these studies, usually less than 1% per year, or less than one species per year, appeared to be due to immigrants that never became established, not due to the extinction of well-established species. More recent studies have revealed similar findings. The take-home message from most studies is that recorded rates of turnover are low, giving little conclusive support to this prediction of the theory of island biogeography. Only one study, carried out by Simberloff and Wilson (1969, 1970), was done with sufficient rigor that it was a good test of whether species turnover occurred, and even this study showed very low levels of turnover (see **Feature Investigation**).

More recent studies have also shown low rates of species turnover. Jorge Rey (1983) defaunated islands of pure salt marsh cordgrass, *Spartina alterniflora*, in north Florida and estimated turnover at only 0.13 species per island per week. Ian Abbott and Robert Black (1980) measured the known extinctions and immigrations of plants on 40 islands off the coast of western Australia. The islands were censused



Feature Investigation

Simberloff and Wilson's Experiments Tested the Predictions of Island Biogeography Theory

Daniel Simberloff and E. O. Wilson conducted possibly the best test of the equilibrium model of island biogeography ever performed using islands in the Florida Keys. They surveyed small red mangrove islands, 11–25 m in diameter, for all terrestrial arthropods. With the help of a pest control company from Miami, they then enclosed each island with a plastic tent and had the islands fumigated with methyl bromide, a short-acting insecticide, to kill all arthropods. The tents were removed, and periodically thereafter Simberloff and Wilson surveyed the islands to examine recolonization rates. At each survey, they counted all the species present, noting any species not there at the previous census and the absence of others that were previously there but had presumably gone extinct (**Figure 21.14**). In this way, they estimated turnover of species on islands.

After 280 days, the islands had similar numbers of arthropod species as before fumigation. The data indicated that recolonization rates were higher on islands nearer to the mainland than on far islands, just as the island biogeography model predicts. However, the data, which consisted of lists of species on islands before and after extinctions, provided little support for the prediction of high turnover. Rates of turnover were low, only 1.5 extinctions per year, compared to the 15–40 species found on the islands within a year. Simberloff (1976) later concluded that turnover probably involves only a small subset of transient species that use islands only as a resting place as they are passing through an area, while the MacArthur-Wilson theory concerns resident species that feed and reproduce on the island.

Simberloff and Wilson also found that most of the species that returned to the islands were the species that had been fumigated. This indicates the existence of biological processes that shaped final community structure the same way every time an island is recolonized, a finding that is contrary to the theory of island biogeography, which treats the dynamics of different colonizing species as equivalent, with community properties essentially unimportant.

sporadically (one to four times between 1956 and 1978). Extinctions and immigrations tended to match each other, but again the majority of turnover was low, with most islands showing turnover rates of between zero and two species per census (or <0.1 species per year). Lloyd Morrison (1997) found low turnover of species on 77 cays in the Bahamas, which he surveyed annually over a 4-year period. Most of the observed turnover (usually $<1\%$ per year or less than one species per year) was due to immigrants that never became established. These studies indicate that recorded rates of turnover are low, which gives little support to the third prediction of the MacArthur-Wilson theory.

In summary, MacArthur and Wilson's equilibrium model of island biogeography has stimulated much research that confirms the strong effects of area and distance on species richness. However, species turnover appears to be low rather than considerable, which suggests that succession on most islands is a fairly orderly process. This means that colonization is not a random process, that the same species seem to colonize first, and that species gradually reappear in the same order.

Check Your Understanding

21.1 Preston (1962) gave the following data for island size and bird species richness in the East Indies.

Island	No. of Bird Species	Area (mi ²)
New Guinea	540	312,000
Borneo	420	290,000
Philippines	368	144,000
Celebes	220	70,000
Java	337	48,000
Ceylon (now Sri Lanka)	232	25,000
Palawan	111	4,500
Flores	143	8,870
Timor	137	18,000
Sumba	108	4,600

Construct a species area curve for these data. Which island is richer in bird species than it should be, based on area alone. Why does Ceylon (now known as Sri Lanka) have more bird species than expected?

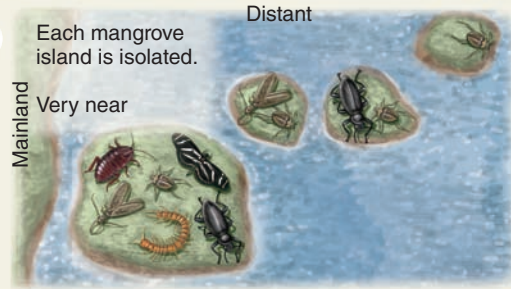
HYPOTHESIS Island biogeography model predicts substantial turnover of species on islands.

STARTING LOCATION Mangrove islands in the Florida Keys.

Conceptual level

Experimental level

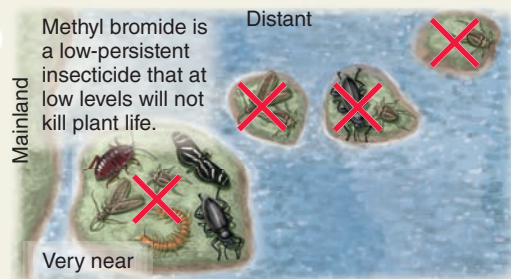
1



Take initial census of all terrestrial arthropods on 4 mangrove islands. Erect framework over each mangrove island.



2



Cover the framework with tent and fumigate with methyl bromide to defaunate island.



3



Remove the tents and conduct censuses every month to monitor recolonization.



4

THE DATA

Island E2 was closest to the mainland and supported the highest number of species. E3 and ST2 were at an intermediate distance from the mainland, and E1 was the most distant.

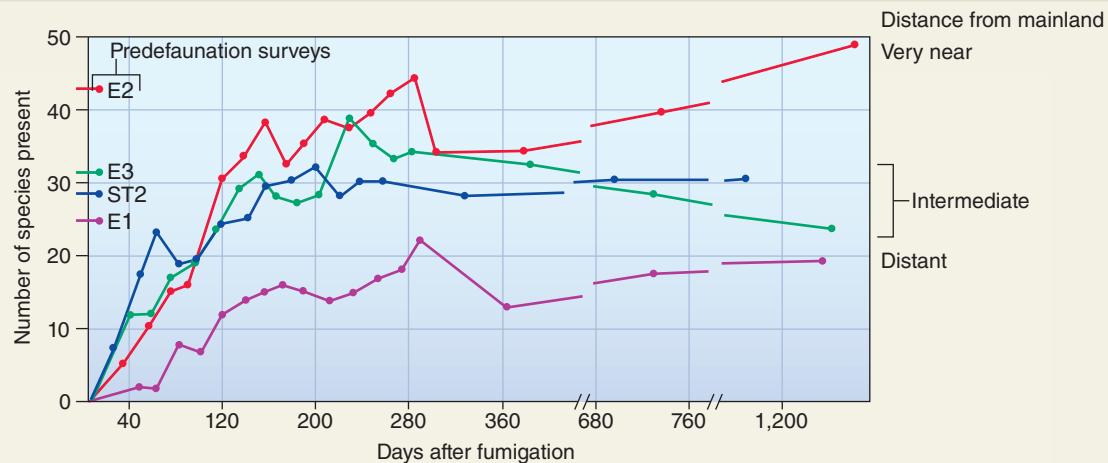


Figure 21.14 Simberloff and Wilson's experiments on species turnover on islands.

21.2 Nature Reserve Designs Incorporate Principles of Island Biogeography and Landscape Ecology

In our exploration of the theory of island biogeography we noted that it could be applied not only to a body of land surrounded by water but also to isolated fragments of habitat. Seen this way, wildlife reserves and sanctuaries are in essence islands in a sea of human-altered land, either agricultural fields or urbanized areas. Conservationists have therefore utilized island biogeography modeling in the concept of nature preserve design. One question for conservationists is how large a protected area should be (**Figure 21.15a**). According to island biogeography, the number of species should increase with increasing area (the species-area effect); thus, the larger the area, the greater the number of species would be protected. In addition, there are other benefits of larger parks. For example, they are beneficial for organisms that require large spaces, including migrating species and species with extensive territories, such as lions and tigers.

Another question is whether it is preferable to protect one single, large reserve or several smaller ones (**Figure 21.15b**). This is called the **SLOSS debate** (for single large or several small). Proponents of the single, large reserve claim that a larger reserve is better able to preserve more and larger popu-

lations, because of lower extinction rates, than an equal area divided into small areas. According to island biogeography, a larger block of equivalent habitat should support more species than all the smaller blocks combined.

However, many empirical studies suggest that multiple small sites of equivalent area will contain more species, because a series of small sites is more likely to contain a broader variety of habitats than one large site. Looking at a variety of sites, researchers Jim Quinn and Susan Harrison (1988) concluded that animal life was richer in collections of small parks than in larger parks. In their study, having more habitat types outweighed the effect of area on species richness. In addition, there may be other benefits of a series of smaller parks, such as a reduction of extinction risk by a single event such as a wildfire or the eruption of disease.

As we learned in Chapter 8, **landscape ecology** is a sub-discipline of ecology that examines the spatial arrangement of elements in communities and ecosystems. In the design of nature reserves, one question that needs to be addressed is how close to situate reserves to each other, such as whether to have three or four small reserves close to each other or farther apart or whether to have a linear or cluster arrangement of small reserves. Island biogeography implies that if an area must be fragmented, the sites should be as close as possible to permit dispersal (**Figure 21.15c,d**). In practice, however, having small sites far apart may preserve more species than having them close together, since once

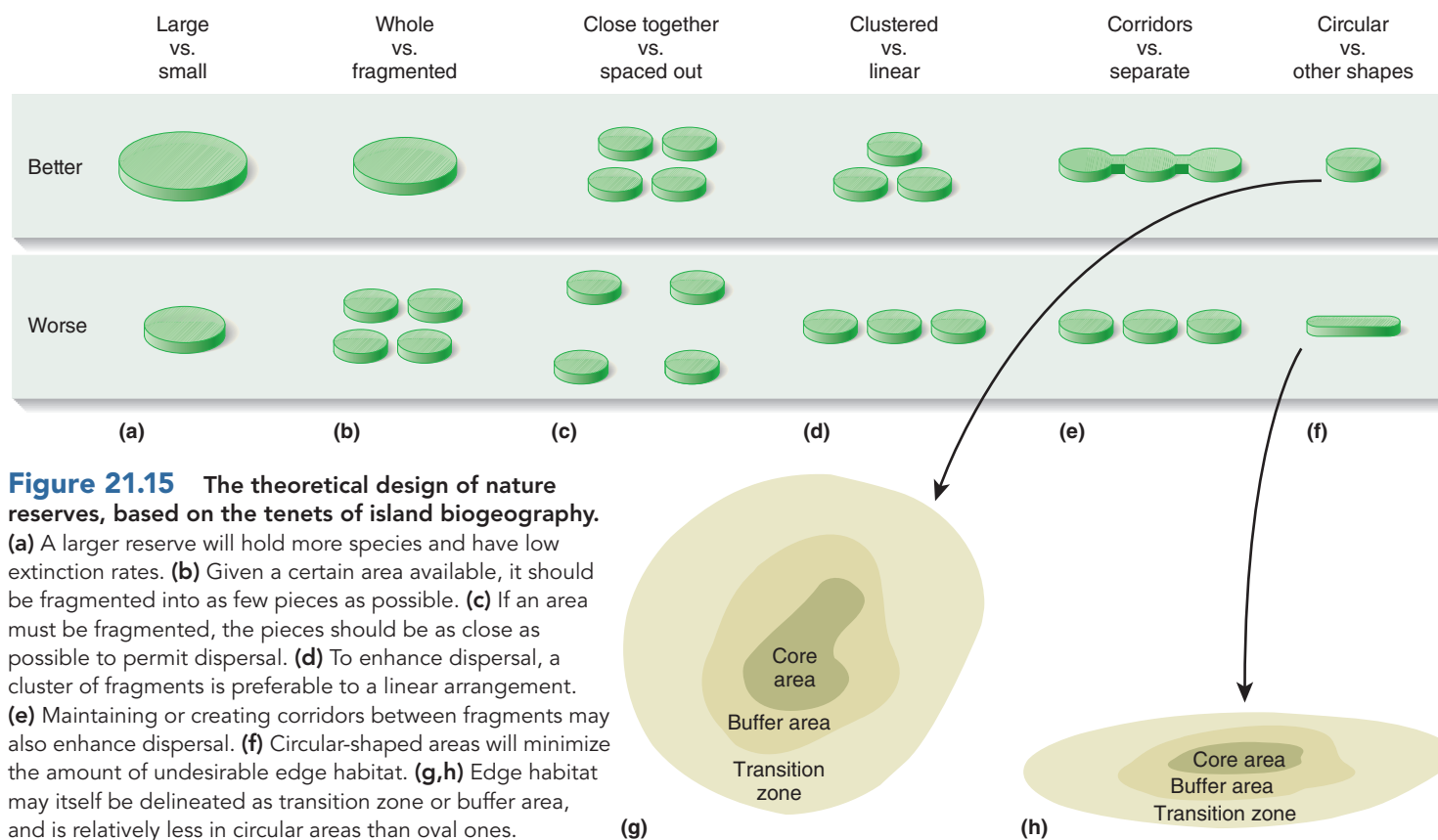


Figure 21.15 The theoretical design of nature reserves, based on the tenets of island biogeography.

(a) A larger reserve will hold more species and have low extinction rates. (b) Given a certain area available, it should be fragmented into as few pieces as possible. (c) If an area must be fragmented, the pieces should be as close as possible to permit dispersal. (d) To enhance dispersal, a cluster of fragments is preferable to a linear arrangement. (e) Maintaining or creating corridors between fragments may also enhance dispersal. (f) Circular-shaped areas will minimize the amount of undesirable edge habitat. (g,h) Edge habitat may itself be delineated as transition zone or buffer area, and is relatively less in circular areas than oval ones.

again, distant sites are likely to incorporate slightly different habitats and thus support a greater mix and higher number of species.

Landscape ecologists have also suggested that small reserves should be linked together by **movement corridors**, thin strips of land that may permit the movement of species between patches (**Figure 21.15e**). Such corridors may facilitate movements of organisms that are vulnerable to predation outside of their natural habitat or that have poor powers of dispersal between habitat patches. In this way, if a disaster befalls a population in one small reserve, immigrants from neighboring populations can more easily recolonize it. This avoids the need for humans to physically move new plants or animals into an area. However, there are disadvantages associated with corridors. First, corridors also can facilitate the spread of disease, invasive species, and fire between small reserves. Second, it is not yet clear if many species would actually use such corridors.

Ellen Damschen and colleagues (2006) used habitat patches in longleaf pine forest, connected and unconnected by corridors, to examine the effects of corridors on plant species richness. The patches had a rich herbaceous understory with over 100 plant species, in contrast to the surrounding dense pine forest. Each landscape consisted of a central 100 × 100-m patch surrounded by four other 100 × 100-m patches situated 150 m away. One of these outlying patches was connected to the central patch by a narrow 150-m corridor. This was the same experiment used by Joshua Tewksbury to examine the effects of corridors on plant and butterfly population densities, and that we described in Chapter 8 (refer back to Figure 8.17). The habitat patches were created in 1999 and surveys revealed the plant community had recovered from the disturbance by 2001. Censuses of all plant species were made from 2001 to 2005, except in 2004, when the U.S. Fish and Wildlife Service burned the site as part of restoration management. Habitat patches connected by corridors retained more plant species than isolated, unconnected patches and this difference increased over time (**Figure 21.16a**). In addition, the corridors did not promote invasion by exotic species (**Figure 21.16b**). Damschen and colleagues attributed the increase in richness in the presence of corridors to increased pollen movement by pollinators and increased seed deposition by seed predators. Both these processes are mediated by animals, and corridors promote animal movement.

Parks are often designed to minimize **edge effects**, the special physical conditions that exist at the boundaries or “edges” of habitats (see **Figure 21.15f**). Habitat edges, particularly those between natural habitats such as forests and developed land, are often different in physical characteristics from the habitat core. For example, the center of a forest is shaded by trees and has less wind and light than the forest edge, which is unprotected. Many forest-adapted species thus shy away from forest edges and prefer forest centers. In many parks, habitat edges may themselves be broken down in transition zones, where some land use, compatible

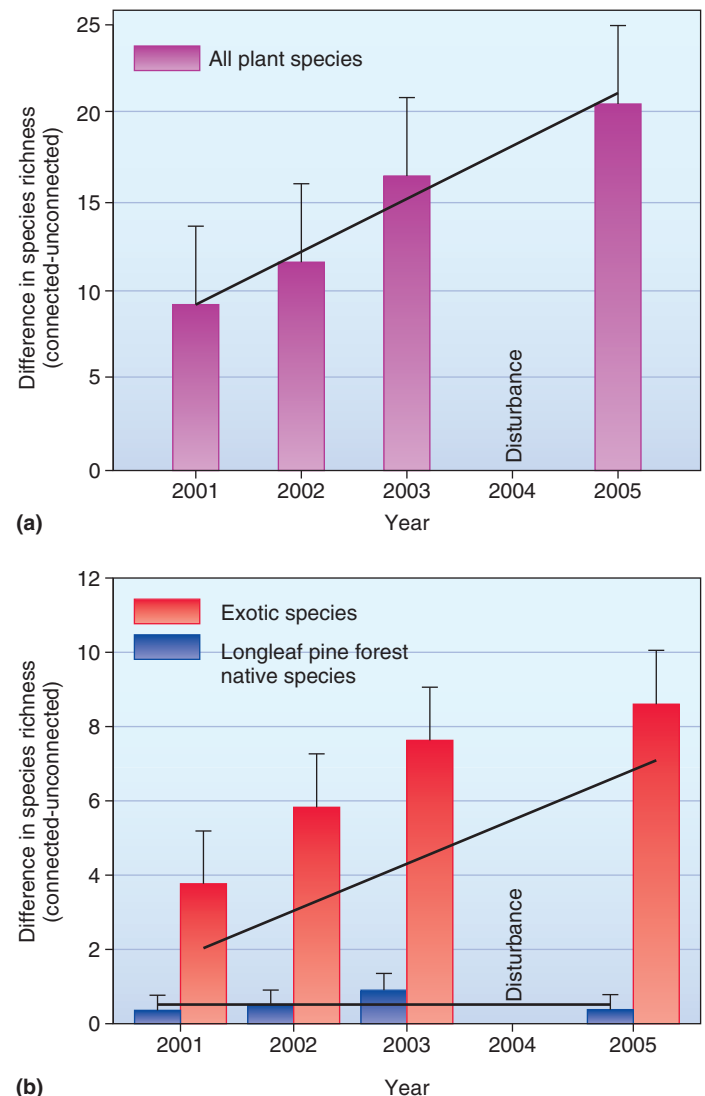


Figure 21.16 The effects of corridors on plant species richness. (a) The difference in plant species richness in patches connected and unconnected by corridors. (b) Differences in species richness in native and exotic species in connected and unconnected patches. (After Damschen, et al., 2006.)

with conservation within the reserve, such as grazing of cattle, but not agriculture, is permitted. Between the transition and the core area is a buffer zone where such activity is not permitted but full use by wildlife does not occur (see **Figure 21.15g**). Circular-shaped parks are preferred over long, skinny parks because the amount of edge is minimized (see **Figure 21.15h**). Although this was not part of the original MacArthur-Wilson theory of island biogeography it is a prominent part of park design. Some conservationists have combined the idea of core areas and corridors by suggesting that corridors should link core areas and consist of core areas themselves.

While the principles of island biogeography theory and landscape ecology are useful in illuminating conservation issues, in reality there is often little choice as to the size,

shape, and location of nature reserves. Management practicalities, costs of acquisition and management, and politics often override ecological considerations, especially in developing countries, where costs for large reserves may be relatively high. Economic considerations often enter into the choice of which areas to preserve. Typically, many countries protect areas in those regions that are the least economically valuable rather than choosing areas to ensure a balanced representation of the country's biota. For example, in the U.S., most national parks have been chosen for their scenic beauty, not because they preserve the richest habitat for wildlife.

When designing nature reserves, countries should also consider how to finance their management. It is interesting that the amount of money spent to protect nature reserves may better determine species extinction rates than reserve size. According to island biogeography theory, large areas minimize the risk of extinctions because they contain sizable populations. In Africa, several parks, such as Serengeti and Selous in Tanzania, Tsavo in Kenya, and Luangwa in Zambia, are large enough to fulfill this theoretical ideal. However, in the 1980s, populations of black rhinoceros and elephants declined dramatically within these areas because of poaching, showing that a wide gap may exist between theory and reality. In reality, the rates of decline of rhinos and elephants, largely a result of poaching, have been related directly to conservation efforts and spending (**Figure 21.17**). The remaining black rhinos, lowland gorillas, and pygmy chimpanzees in Africa and the vicuna, a llama-like animal in South America, have all shown the greatest stabilization of numbers in areas that have been heavily patrolled and where resources have been concentrated.

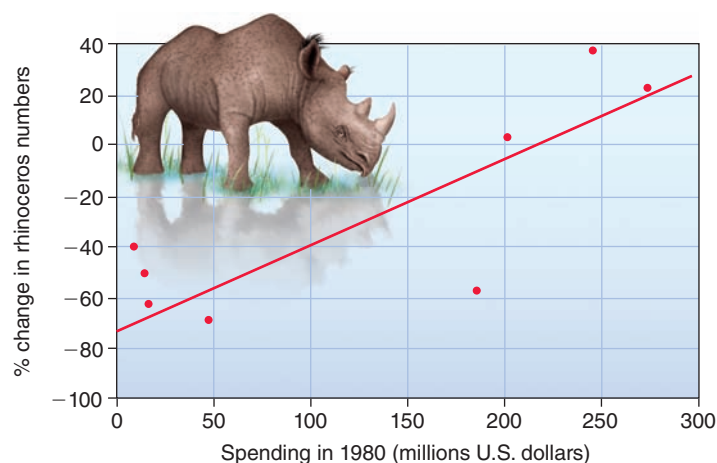


Figure 21.17 The economics of conservation. A positive relationship is seen between change in black rhinoceros numbers between 1980 and 1984, and conservation spending in various African countries. (After Leader-Williams and Albon, 1988.)

Check Your Understanding

21.2 An area of habitat is reduced from 1,000 to 500 hectares. If $c = 10$ and $z = 0.3$, what percent of species is lost?

SUMMARY

- Species succession on islands after a disturbance is influenced by mode of dispersal (Figure 21.1).
- In the theory of island biogeography, the number of species on an island tends toward an equilibrium number determined by the balance between immigration rates and extinction rates (Figure 21.2).
- Some habitat patches on mainland areas can be viewed as habitat islands in a sea of unsuitable habitat (Figure 21.3).
- The theory of island biogeography predicts that the number of species increases with increasing island size, that the number of species decreases with distance from the source pool, and that there is frequent turnover of species (Figure 21.4).
- Much evidence exists to support the species-area effect (Figures 21.5, 21.6, 21.8).
- The nature of the relationship between species richness and area can be simultaneously affected by many factors

including habitat productivity and the taxon of interest (Figure 21.7).

- Experimental reduction of island area in the Florida Keys caused a reduction in species richness, supporting the species-area effect (Figure 21.9).
- Species loss during deforestation may be predicted using species-area relationships (Figure 21.10).
- Much evidence also supports the species-distance effect (Figures 21.11–21.13).
- Evidence suggests species turnover is minimal (Figure 21.14).
- The principles of island biogeography can be applied to the design of nature reserves (Figure 21.15).
- The richness of some areas is increased by the presence of corridors (Figure 21.16).
- In terms of park management, practicalities often override ecological considerations (Figure 21.17).

TEST YOURSELF

1. On which type of island would you expect species richness to be greatest?
 - a. Small, near mainland
 - b. Small, distant from mainland
 - c. Large, near mainland
 - d. Large, distant from mainland
2. The relationship between species richness and island area is described by the equation:
 - a. $S = A^{cz}$
 - b. $A = cS^z$
 - c. $S = cA^z$
 - d. $c = AS^z$
 - e. $S = AC^z$
3. Which is part of the original MacArthur-Wilson theory of island biogeography?
 - a. \hat{S} is increased by distance from the source pool
 - b. \hat{S} is decreased by island size
 - c. \hat{S} is a balance between immigration and extinction
 - d. Island size influences immigration rates
 - e. Distance from source pool influences extinction rates
4. According to MacArthur and Wilson's equilibrium model of island biogeography, which of the following nature reserve designs is favored?
 - a. Small
 - b. Fragmented
 - c. Oval shaped
 - d. With corridors
5. The acronym SLOSS stands for:
 - a. Several large or single small
 - b. Single large or several small
 - c. Single large or single small
 - d. Several large or several small
6. In the MacArthur-Wilson theory of island biogeography, z represents:
 - a. The number of species
 - b. A constant measuring number of species per unit area
 - c. A constant measuring slope
 - d. The intercept
 - e. Area
7. Why are the immigration and extinction lines in the MacArthur-Wilson model both curved?
 - a. Species arrive at different rates
 - b. Some organisms are more mobile than others
 - c. Competition increases as more species arrive
 - d. Later arriving species tend to be better competitors
 - e. All of the above
8. Habitat islands on the mainland tend to have lower z values than true islands.
 - a. True
 - b. False

CONCEPTUAL QUESTIONS

1. What were the main tenets of the MacArthur-Wilson theory of island biogeography?
2. What evidence is there to support the MacArthur-Wilson theory of island biogeography and what evidence is there to contradict it?
3. Discuss the application of island biogeography to nature reserve design.

DATA ANALYSIS

William Tonn and John Magnuson investigated the number of fish species, lake area, and other habitat variables, including vegetation diversity, measured as H_s , from 18 shallow lakes in Wisconsin. Plot the number of fish species against the \log_{10} lake area and against vegetational diversity. What can you conclude?

Lake	Area (ha)	Vegetation diversity, H_s	Species richness
1	76.1	1.69	9
2	38.0	1.62	8
3	4.9	0.37	4
4	5.7	1.08	4
5	3.2	0.93	6
6	42.9	1.47	10
7	9.7	0.58	10
8	89.0	0.78	6
9	23.9	0.91	5
10	19.0	0.50	7
11	53.0	0.96	7
12	8.1	0.65	7
13	44.5	1.55	8
14	6.1	0.00	3
15	89.8	0.91	6
16	3.2	0.35	2
17	2.4	0.40	2
18	2.8	0.32	1



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SECTION SIX

Biomes

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Chapter 24 Freshwater Biomes 500

The Earth from space. The Earth supports an array of life-forms existing in areas as diverse as tropical rain forests, hot deserts, and open oceans.