Model Presentation and Predictions

THE SPECIES–AREA RELATIONSHIP

One of the few genuine "laws" in ecology is the **species–area relationship**: large islands support more species than small islands. The pattern holds for most assemblages of organisms, everything from vascular plants of the British Isles to reptiles and amphibians of the West Indies. The "islands" need not even be oceanic. Fish that live in lakes, mammals that occupy patches of forested mountaintops, and insects that visit thistle-heads all show a species–area relationship for their respective habitat islands. Because a national park or a nature reserve effectively is an island in a sea of disturbed habitat, studies of the species–area relationship may be relevant to the preservation of species in a fragmented landscape. This chapter explores in detail the relationship between area and the number of species in the community (species richness).

Figure 7.1a shows a typical species–area relationship for species of breeding land-birds on islands of the West Indies. The x axis shows the area of island, and the y axis shows the number of breeding land-bird species. You can see that the relationship is not linear: species number increases rapidly with area for small islands, but more slowly for large islands. For many oceanic islands, a rule of thumb (**Darlington's Rule**) is that a tenfold increase in island area results in a doubling of species number (Darlington 1957). Mathematically, the species–area relationship for many communities can be described by a simple power function:

$$S = cA^z \qquad \text{Equation 7.1}$$

In this equation, S is the number of species, A is the island area, and z and c are fitted constants, which we will explain in a moment. If we take the logarithm (base 10) of each side of the equation, we have:

$$\log(S) = \log(c) + z\log(A) \qquad \text{Equation 7.2}$$

The logarithmic transformation turns the species–area curve into a straight line when plotted on logarithmic axes. The constant $\log(c)$ is the intercept of that line, and the constant z is the slope of the line. Figure 7.1b shows the West Indian bird data replotted with both axes transformed to logarithms. The data conform fairly well to a straight line, suggesting a good fit to the power function.
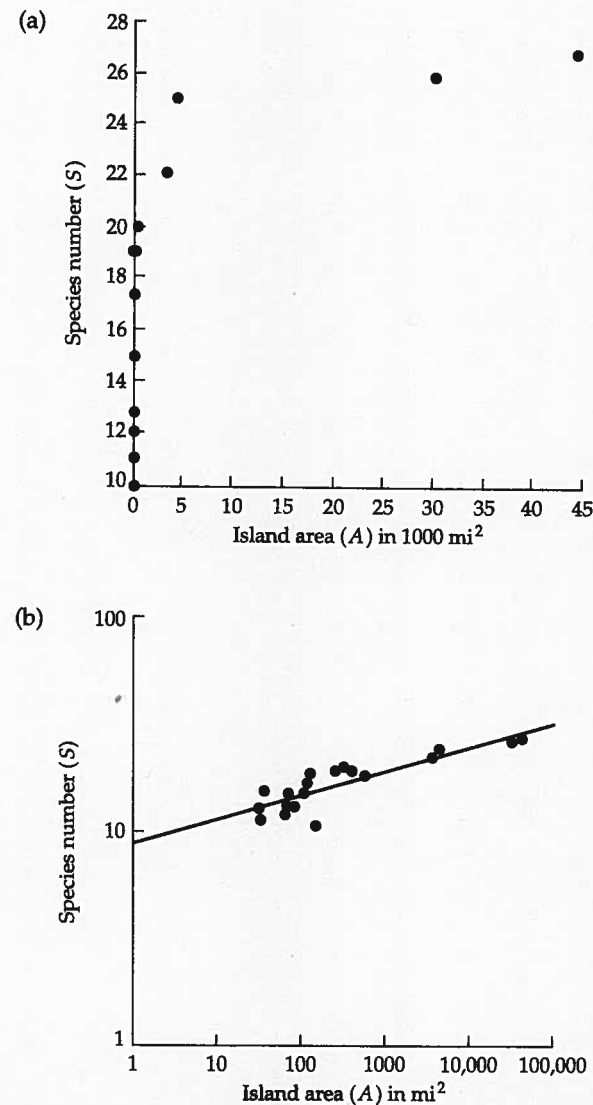
Figure 7.1 (a) Species–area relationship for breeding land-birds of the West Indies. Each point is a different island. Note that species number increases rapidly for small islands, but more slowly for large islands. (Data from Gotelli and Abele 1982.) (b) Logarithmic (base 10) transformation of the species–area relationship. The data in (a) have been plotted on a double-log plot. The best-fitting power function is shown by the straight line $\log(S) = 0.942 + 0.113 \log(A)$. Equivalently, the power function is $S = 8.759(A)^{0.113}$.

The area of an island is not the only factor that affects species richness. Figure 7.2 shows the effects of distance on species richness for birds of the Bismarck Islands in the tropical Pacific. New Guinea serves as the probable "source pool" for these islands, because all of the bird species found on the Bismarck Islands are a subset of the New Guinea avifauna. The x axis of this graph gives the distance from each island to New Guinea. The y axis shows the observed number of species divided by the number expected for a "near" island (<500 km from New Guinea) of comparable area. You can see that relative species richness decreases with increasing distance from the source pool. In general, species richness is reduced for communities in small or isolated areas. In the following sections, we develop several models that attempt to explain the **area effect** (more species on large islands than on small islands) and the **distance effect** (more species on near islands than on far islands).

THE HABITAT DIVERSITY HYPOTHESIS

The most straightforward explanation for the species–area relationship is that large islands contain more habitat types than small islands. Therefore, species that are restricted to certain habitat types may occur only on large islands with those habitats. The species–area relationship for West Indian land-birds can be
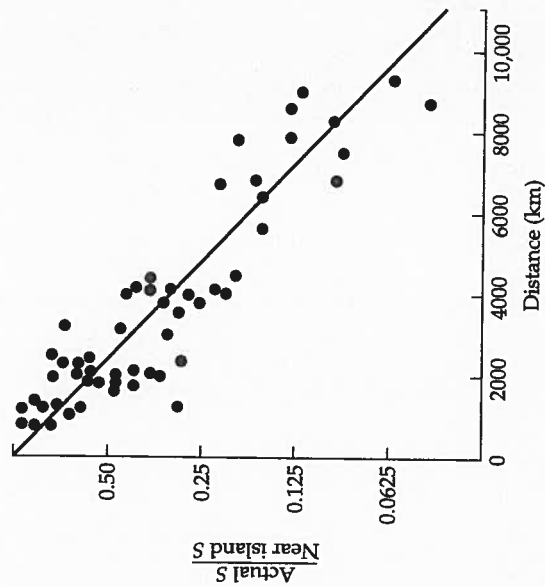

Figure 7.2 Distance effects for birds of the Bismarck Archipelago. The x axis gives the distance from each island to New Guinea, the presumed source pool. The y axis shows the observed species richness divided by the expected species richness for a "near" island (<500 kilometers from New Guinea) of comparable size. (From Diamond 1972.)

explained, in part, by this phenomenon. The largest islands in the chain are the Greater Antilles (Puerto Rico, Cuba, Hispaniola, and Jamaica). These islands include many unique habitat types, such as extensive swampland (Cuba) and high-elevation pine forest (Hispaniola), that do not occur on any of the smaller islands. Habitat specialists such as the Zapata wren of Cuba (*Ferminia cerverai*) and the white-winged crossbill of Hispaniola (*Loxia leucoptera*) occur only in these particular habitats. Intermediate-sized islands, such as Guadeloupe and St. Lucia, are steep volcanic plugs that have fewer habitats and species than islands of the Greater Antilles. Some of the smaller islands, such as Antigua and Barbuda, are flat coral atolls. They are arid islands with structurally simple vegetation, and they support even fewer bird species.

Although habitat diversity can account for many species–area relationships, it is not always the correct explanation. For one thing, most species are not extreme habitat specialists, and their distribution may not always be limited by available habitat. In addition, there are many examples of species–area relationships in which there is little, if any, habitat variation. Within patches of identical habitat, species number is still greater on large islands than small, suggesting that other forces may be at work. In the next section, we develop the "equilibrium model" of island biogeography as an alternative hypothesis that accounts for the species–area relationship. Later in this chapter, we describe a third hypothesis, the passive sampling model, which can also explain the species–area relationship.

THE EQUILIBRIUM MODEL OF ISLAND BIOGEOGRAPHY

The **equilibrium model of island biogeography** was popularized by Robert H. MacArthur (1930–1972) and Edward O. Wilson (1929–). It is sometimes referred to as the "equilibrium model" or the "MacArthur–Wilson model." The model's basic premise is that the number of species occurring on an island represents a balance between recurrent *immigration* of new species onto the island, and recurrent *extinction* of resident species (MacArthur and Wilson 1963, 1967). When immigration and extinction rates are equal, the number of species is at an equilibrium. The concept is similar to the equilibrium N in a local population (Chapter 2), and to the equilibrium fraction of sites occupied by a metapopulation (Chapter 4).

The equilibrium model assumes there is a permanent mainland **source pool** of species that can potentially colonize an island. There are P species in the mainland pool, and we assume for now they are all similar to one another in colonization and extinction potential. We define the **immigration rate**, λ_s, as the number of new species colonizing the island per unit time. The **extinction rate**, μ_s, is the number of species already present on the island going extinct per unit time. The rate of change in species number on the island (dS/dt) is the difference between the immigration rate and the extinction rate.

Thus:

$$\frac{dS}{dt} = \lambda_s - \mu_s \qquad \text{Equation 7.3}$$

First, we will define the functions for λ_s and μ_s. Next, we will set Equation 7.3 equal to zero and solve for the equilibrium number of species. Finally, we will modify the extinction and immigration curves to account for the effects of area and isolation on species richness.

Figure 7.3 illustrates the immigration curve for the equilibrium model. The x axis of the graph shows the number of species present on the island. The y axis shows the rate of immigration. The **maximum immigration rate, I,** occurs when the island is empty. This is because as more species are present, fewer *new* species are added to the island. This is because as more species are present, fewer *new* species remain in the source pool as potential colonists. Finally, suppose that all of the species in the source pool are present on the island. By definition, there can be no further immigration, so the immigration curve crosses the x axis at the point $S = P$. Thus, the immigration curve is a decreasing straight line, with a maximum rate of I, and a minimum rate of zero, when $S = P$.

Remember that a straight line can be described by the equation $y = a + bx$, where a is the intercept and b is the slope. In this case, the intercept is I, and the slope (rise over run) is $-I/P$. Thus, the equation for the immigration rate is:

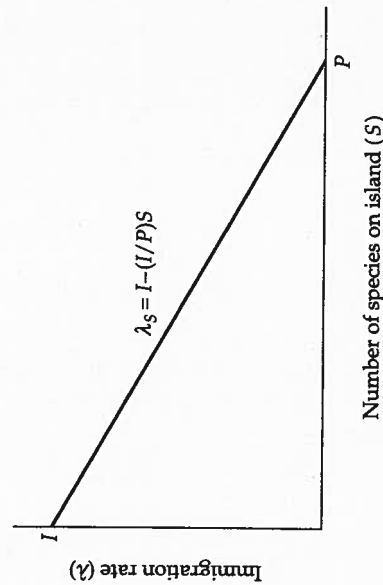$$\lambda_s = I - \left(\frac{I}{P}\right)S \qquad \text{Expression 7.1}$$

Figure 7.3 The immigration rate in the MacArthur–Wilson model. The immigration rate (number of species per unit time) decreases as more species are added to the island.

Now we turn to the extinction rate, μ_s. We expect μ_s to *increase* with increasing S: the more species present on the island, the greater the rate at which species disappear. This relationship occurs because each species has a constant probability of disappearance, so species disappear at a faster rate when there are more species present on the island. The **maximum extinction rate,** E, will occur when all the species in the source pool are present on the island ($S = P$). Conversely, if no species are present on the island ($S = 0$), the extinction rate must equal zero. Thus, the extinction curve is also a straight line with an intercept of zero, and a maximum rate of E, which occurs when $S = P$ (Figure 7.4):

$$\mu_s = \left(\frac{E}{P}\right)S \qquad \text{Expression 7.2}$$

Now that we have derived expressions for linear immigration and extinction rates, we can substitute these into Equation 7.3 to model the change in species richness on an island:

$$\frac{dS}{dt} = I - \left(\frac{I}{P}\right)S - \left(\frac{E}{P}\right)S \qquad \text{Expression 7.3}$$

The number of species on an island reaches an equilibrium when (dS/dt) equals zero. Setting Expression 7.3 equal to zero and solving for S yields:

$$S\left(\frac{I+E}{P}\right) = I \qquad \text{Expression 7.4}$$
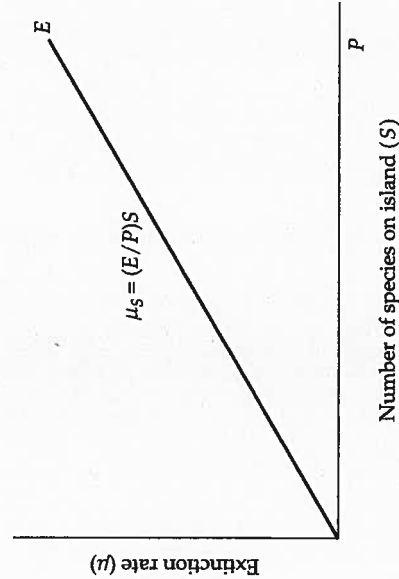

Figure 7.4 The extinction rate in the MacArthur–Wilson model. The extinction rate (number of species extinctions per unit time) increases as more species are added to the island.

The equilibrium number of species, $\hat{S}$, is thus:

$$\hat{S} = \frac{IP}{I+E} \qquad \text{Equation 7.4}$$

The equilibrium depends on the size of the source pool (P) and the maximum immigration (I) and extinction (E) rates. Graphically, this equilibrium species number corresponds to the point on the x axis beneath the intersection of the immigration and extinction curves (Figure 7.5). At the intersection, the rate at which new species arrive is matched by the rate at which species present on the island go extinct.

This equilibrium point is stable. If we are below $\hat{S}$, we are to the left of the intersection point. In this region of the graph, the immigration rate exceeds the extinction rate, so species number increases. To the right of the intersection, extinctions exceed immigrations, so species number declines.

Equation 7.4 shows that species richness is increased by larger source pools and higher immigration rates, and decreased by higher extinction rates. Note the similarity between this equilibrium and the equilibrium in the island–mainland metapopulation model (Equation 4.4) we derived in Chapter 4. The intersection of the immigration and extinction curves also resembles the intersection of density-dependent birth and death rate curves in our derivation of the logistic growth equation (Figure 2.1) in Chapter 2.

Figure 7.5 also shows that the equilibrium is characterized by a **turnover rate**, which is measured on the y axis of the equilibrium graph. This turnover rate, T, is the number of species arriving (or disappearing) per unit time at equilibrium. T can be measured as either the extinction or the immigration rate, because these two are equal at equilibrium. Using some simple geometry, we see in Figure 7.5 that:

$$\frac{\hat{T}}{\hat{S}} = \frac{E}{P} \qquad \text{Expression 7.5}$$

Therefore:

$$\hat{T}P = \hat{S}E \qquad \text{Expression 7.6}$$

Rearranging and substituting Equation 7.4 for $\hat{S}$ gives:

$$\hat{T} = \frac{\left(\dfrac{IP}{I+E}\right)E}{P} \qquad \text{Expression 7.7}$$
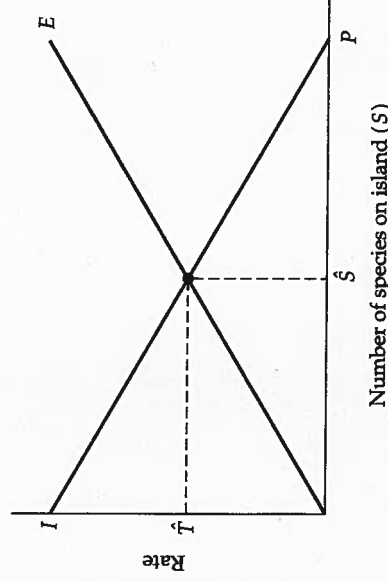
Figure 7.5 Equilibrium species number in the MacArthur–Wilson model. The intersection of the immigration and extinction curves determines the equilibrium number of species ($\hat{S}$) and the turnover rate ($\hat{T}$) at equilibrium.

$$\hat{T} = \frac{IE}{I+E} \qquad \text{Equation 7.5}$$

Note that the turnover rate at equilibrium depends only on the maximum immigration and extinction rates (I and E), not on the size of the source pool (P). As you might expect, increasing either the maximum immigration or extinction rate increases the turnover at equilibrium.

This turnover of island populations at equilibrium is a key feature of the MacArthur–Wilson model. In contrast to many of the ecological models we have studied, the MacArthur–Wilson model does not predict stable populations. Instead, there is ongoing colonization and stochastic extinction of island populations. Species composition on the island is continually changing, although total species number remains relatively constant.

So far, we have constructed an equilibrium model of island species richness, but we still haven't explained the species–area effect. To do so, we must incorporate two additional assumptions about the demography of the colonizing species. The first assumption is that total population size for each species is proportional to island area. In other words, the *density* of populations (number of individuals per unit of area) is the same on islands of different size. The second assumption is that the probability of population extinction decreases with increasing population size. This assumption follows directly from the model of demographic stochasticity developed in Chapter 1. Because population sizes will be larger on big islands than on small islands, the extinction rates will correspondingly be lower on big islands.
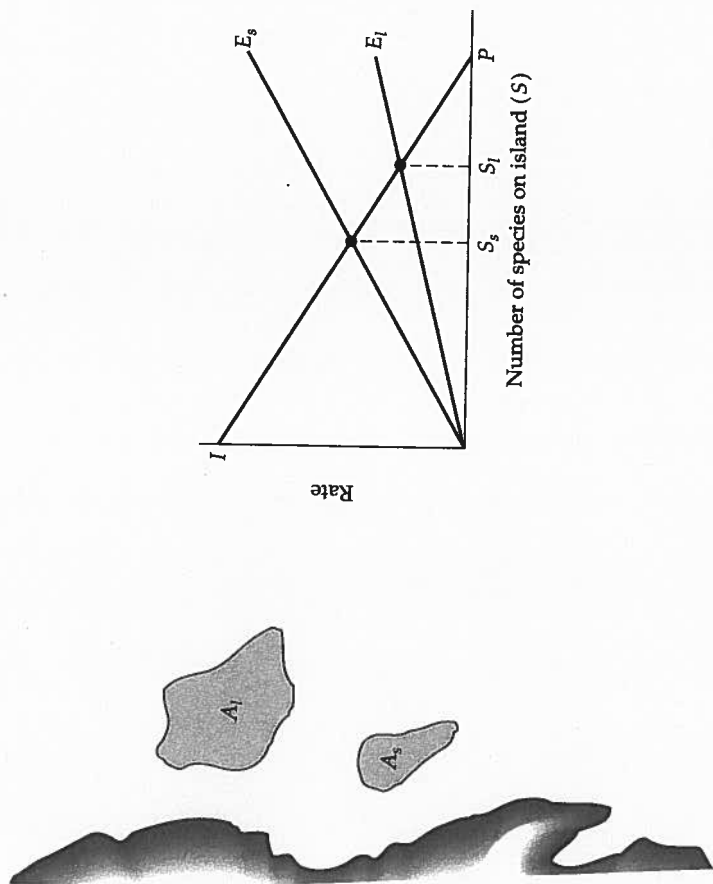
Figure 7.6 The area effect in the MacArthur–Wilson model. Smaller islands have smaller population sizes, which increases the extinction rate and leads to a lower species equilibrium. E_s is the maximum extinction rate for small islands; E_l is the maximum extinction rate for large islands.

Suppose we have a large island (A_l) and a small island (A_s) that differ only in area, but are identical in habitat diversity and distance from the source pool (Figure 7.6). Because both islands are equidistant from the mainland and colonized by the same source pool of P species, they have the same immigration curve. However, maximum extinction rates on the large island (E_l) are lower than on the small island (E_s) because population sizes are greater on the large island. Because of this area effect, the equilibrium number of species is greater on the large island, with a lower rate of turnover.

We can also account for the distance effect by modifying the immigration curves for near and distant islands. Suppose two islands have identical areas and habitats, but differ in their distance from the source pool (Figure 7.7). Because the areas are equal, the two islands have the same extinction curve. But the maximum immigration rate will be higher on the near island (I_n) than
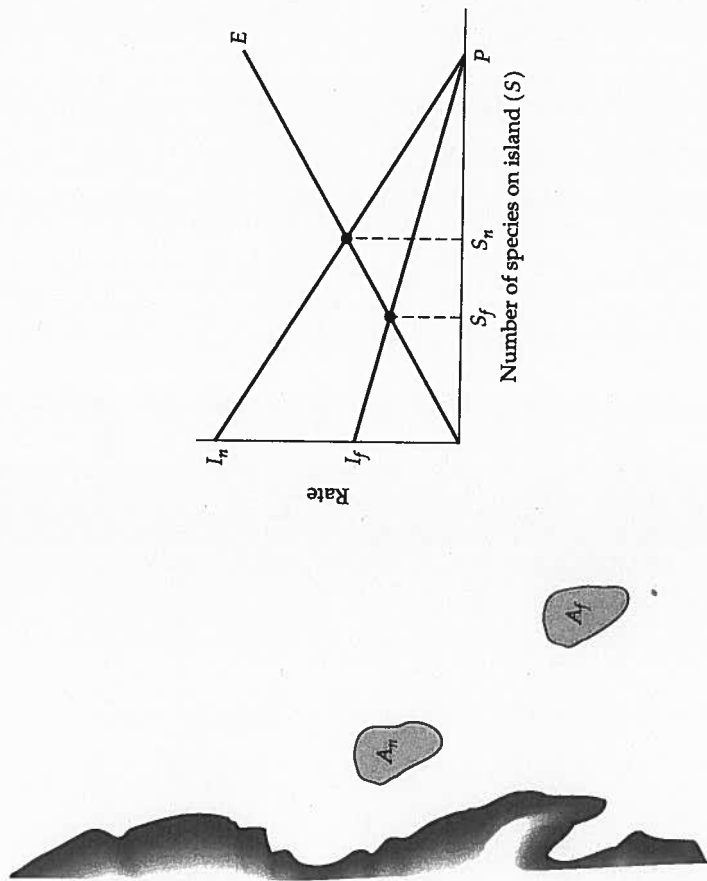
Figure 7.7 The distance effect in the MacArthur–Wilson model. Islands that are distant or isolated from the source pool have a reduced immigration rate, leading to a lower species equilibrium. I_n is the maximum immigration rate for near islands; I_f is the maximum immigration rate for far islands.

on the far island (I_f). Consequently, the near island will have more species at equilibrium than the far island. The near island will also be characterized by greater turnover than the far island.

Thus, island species richness in the MacArthur–Wilson model is uniquely determined by the geometry of an island—its area determines the extinction rate, and its distance or isolation determines its immigration rate. The intersection of these two curves controls the equilibrium number of species and the turnover rate.

Model Assumptions

Although the equilibrium model predicts patterns of species richness, its underlying assumptions are at the population level. These assumptions are:

✔ *An island potentially can be colonized by a set of P source pool species that have similar colonization and extinction rates.* This assumption implies that the species in the source pool and on the island are not undergoing any evolutionary change that might alter colonization or extinction rates. Thus, like most ecological models, the equilibrium model does not incorporate evolutionary mechanisms or historical constraints that might influence species richness.

✔ *The probability of colonization is inversely proportional to isolation or distance from the source pool.* Isolated islands have shallower immigration curves than non-isolated islands. All other things being equal, this lowers the equilibrium number of species (see Problem 7.2).

✔ *The population size of a given species is proportional to the area of the island.* In other words, the density of each population (number of individuals/area) is constant throughout the archipelago. Alternative models (Schoener 1976) assume that competitive interactions are important, so that both island area and species richness influence population size.

✔ *The probability of a population becoming extinct is inversely proportional to its size.* Although the equilibrium model does not explicitly forecast population sizes, this assumption incorporates the idea that demographic stochasticity (see Chapter 1) increases the risk of extinction at small population sizes. This assumption and the previous one ensure that extinction curves are steeper for small islands than they are for large islands, leading to a species-area curve.

✔ *Colonization and extinction of local populations is independent of species composition on the island.* In contrast to classic models of competition (Chapter 5) and predation (Chapter 6), the equilibrium model assumes that the presence of one species does not affect the colonization or extinction of another. If extinctions are independent of species composition, the island community is "non-interactive." If colonizations are independent, the island community is not undergoing any successional change, because the particular order of arrival and departure of species is not important.

Model Variations

NONLINEAR IMMIGRATION AND EXTINCTION CURVES

The linear immigration curve implies that all species have identical potential for dispersal and colonization of islands. But suppose that some species are
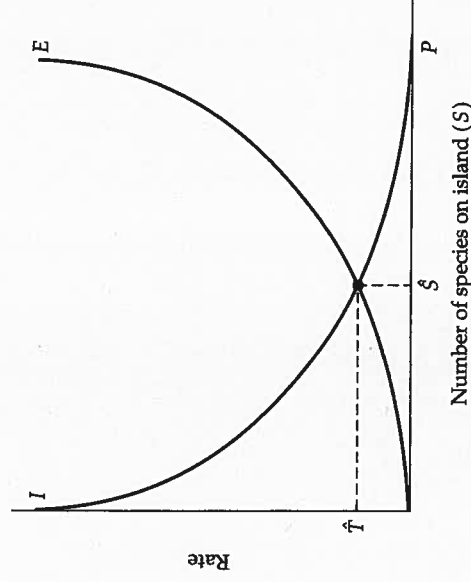
Figure 7.8 Nonlinear immigration and extinction curves in the MacArthur–Wilson model. These curves may reflect the influence of species interaction on the extinction rate and differential colonization ability on the immigration rate. The qualitative predictions of this nonlinear model are similar to those of the linear model described in the text (Figure 7.5).

much better at dispersal and colonization than others. These species would be among the first to colonize an empty island, whereas the poor dispersers would arrive later in the colonization sequence. With differential dispersal, the immigration curve would be exponential, with a steep decline initially and a slower rate of decrease as later species are added (Figure 7.8).

Similarly, the linear extinction curve implies that species extinctions are independent of one another. It might be more realistic to assume that competition increases the extinction rate when more species are present. In this case, the extinction curve would increase exponentially with S (Figure 7.8). In textbooks, the MacArthur–Wilson model is usually presented with these nonlinear immigration and extinction curves. Fortunately, the basic predictions of the equilibrium model remain the same, whether the linear or nonlinear rate curves are used.

AREA AND DISTANCE EFFECTS

Both area and distance affect extinction and immigration in the MacArthur–Wilson model. But the basic model describes only two mechanisms: the effect of area on extinction, and the effect of distance on immigration (Figure 7.9). In the next two sections, we briefly explore the effect of distance on extinction (the "rescue effect"), and the effect of island area on immi-