

8

SPECIES-AREA RELATIONSHIPS

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In Chapter 7, we pointed out that a major difficulty in assessing co-occurrence patterns was variation in site quality. If some sites are more favorable than others for all species, patterns of species aggregation will emerge that do not reflect interspecific interactions (Pielou and Pielou 1968). Variation in site quality is often manifest in total species richness, which should be controlled for in null models of species co-occurrence (Connor and Simberloff 1979).

But why is species richness greater in some sites than in others? This question is an important one that has been studied independently of factors that determine co-occurrence. Area is the most basic correlate of species richness. Large areas support more species than small areas, although the relationship is rarely linear. For oceanic archipelagoes, species number roughly doubles for every tenfold increase in island area (Darlington 1957). The species-area relationship is most obvious when the “sites” are true islands (Figure 8.1). For example, mammalian species richness is well correlated with area in archipelagoes of oceanic, land-bridge, coastal, and river islands (Wright 1981; Lomolino 1984).

Species richness also correlates with the area of most insular patches of habitat. Familiar examples include mammals of forested mountaintops (Brown 1971), decapod crustaceans of pocilloporid coral heads (Abele 1976), and insects of thistleheads (Brown and Kodric-Brown 1977). “Areas” need not even be insular. Species number is related to area for vascular plants of different-sized quadrats (Connor and McCoy 1979), lumbricid earthworms of European sites (Judas 1988), and parasitic fungi of British trees, where area was defined as the geographic range of the host plant species (Strong and Levin 1975). Species-area relationships hold for tropical and temperate archipelagoes (Schoener 1976b) and for fossil and extant assemblages of entire continents (Flessa 1975).

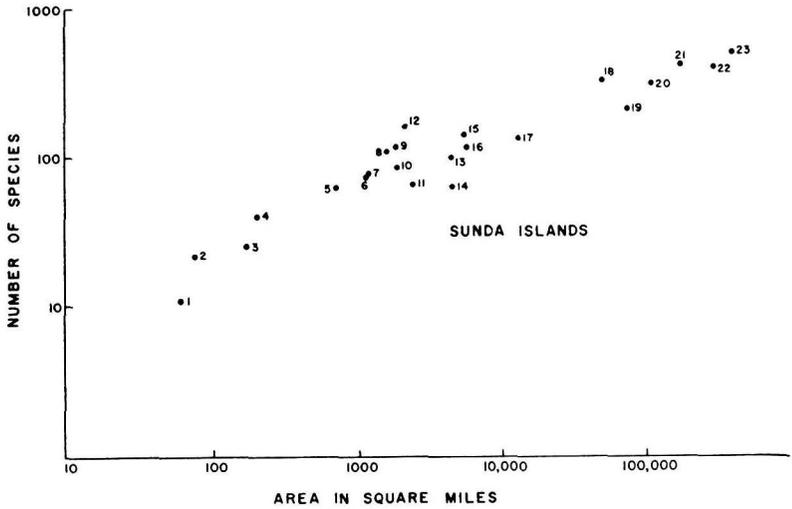


Figure 8.1. Species-area relationship for land and water birds of the Sunda Islands. Numbers indicate different islands (1 = Christmas Island, 23 = New Guinea). Note the logarithmic transformation of both axes. Data such as these were used to support the equilibrium model, although other models may account for the species-area relationship as well. From MacArthur and Wilson (1963), with permission.

“One of ecology’s few genuine laws” (Schoener 1976b), the species-area relationship has been described and interpreted for over 120 years (McGuinness 1984a), but there is little agreement on its cause. Some authors have viewed it as a dynamic balance between immigration and emigration (MacArthur and Wilson 1963, 1967) that may ultimately reflect energetic constraints on community development (Wright 1983). Because of their insularity, nature reserves have been likened to islands, and species-area curves have formed the basis for conservation strategy (Wilson and Willis 1975). Others have suggested that the species-area relationship embodies little more than a passive sampling effect and may have no biological significance (Connor and McCoy 1979). A null model that treats islands as targets and individuals as passive propagules incorporates minimal biological forces, but may account for the species-area relationship (Arrhenius 1921; Coleman 1981; Coleman et al. 1982). In this chapter, we review four hypotheses that have been put forth to explain the species-area relationship, discuss other patterns that are predicted by these mechanisms, and describe the use of null models in understanding species-area curves.

WHAT MECHANISMS ACCOUNT FOR SPECIES-AREA CURVES?

In spite of the generality of the species-area relationship, it is likely to result from a variety of forces that reflect the sampling properties of islands, habitat variability, population processes, and the underlying species abundance distribution (Figure 8.2). To date, four distinct mechanisms have been proposed to account for the species-area relationship. These mechanisms are not mutually exclusive, but they do emphasize different processes that can cause a correlation between species richness and area:

1. *The disturbance hypothesis.* Disturbances that reduce species diversity are more common on small islands than on large islands (McGuinness 1984a).
2. *The habitat diversity hypothesis.* Large areas contain more habitats and hence more species (Williams 1943).
3. *The passive sampling hypothesis.* Large areas function as “targets” that sample more individuals, and hence more species (Arrhenius 1921; Coleman 1981; Coleman et al. 1982).
4. *The equilibrium hypothesis.* Large areas support larger population sizes of all resident species than do small islands. Consequently, the probability of stochastic extinction is reduced on large islands (Munroe 1948; Preston 1962; MacArthur and Wilson 1963, 1967).

Figure 8.2. Mechanisms controlling the relationship between area and species number. Several mechanisms may contribute to the apparently straightforward correlation between S and A . From Haila (1983), with permission.

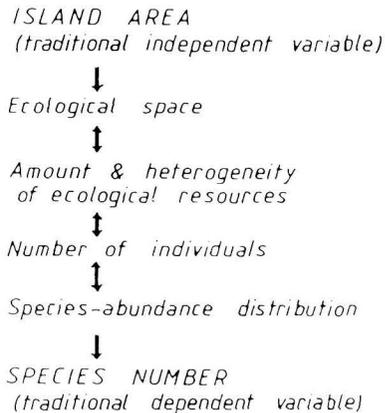


Table 8.1

Predicted patterns for hypotheses that explain the species-area relationship

Pattern	Equilibrium hypothesis	Habitat diversity hypothesis	Passive sampling hypothesis	Disturbance hypothesis
Substantial turnover	Yes	Yes or no	No	Yes (small islands)
<i>S</i> - <i>A</i> correlation for equal-sized quadrats	Yes	No	No	No
Fit with passive sampling model	Yes or no	Yes or no	Yes	Yes or no
Fit with habitat-unit model	No	Yes	No	No

These hypotheses have not received equal attention in the literature. The disturbance hypothesis, for example, was offered as an explanation for species-area relationships only in the 1980s (McGuinness 1984a). And although the passive sampling hypothesis was first introduced more than 70 years ago (Arrhenius 1921), it has only recently been employed as a null model for the species-area relationship. The equilibrium hypothesis, as popularized by MacArthur and Wilson (1967), dominated the literature in the 1960s and 1970s, and was often accepted without adequate proof (Williamson 1989). Gilbert (1980) reviewed the uncritical acceptance of the theory during this period, and Boecklen and Simberloff (1986) discussed its premature application to the design of nature reserves, through “faunal collapse” and “relaxation” models.

The essential problem was that many authors viewed the species-area relationship as sufficient evidence for the equilibrium theory, without a critical evaluation of the alternatives. Although the four hypotheses all predict a species-area relationship, each has a different set of assumptions and a unique set of additional predictions (Table 8.1). In the following sections, we review the assumptions, predictions, and critical tests of each hypothesis. Next, we explain how null models have been used to examine two particular species-area patterns: (1) the slope of the species-area regression, which has been interpreted as a measure of isolation, and (2) the constancy of species number (*S*) through time, which has been taken as an indicator of equilibrium status.

THE DISTURBANCE HYPOTHESIS

If small islands are disproportionately subject to chronic disturbances that remove species, then a species-area relationship will result (McGuinness 1984a). This hypothesis assumes that small islands are more vulnerable to disturbance, and that species richness increases as disturbance frequency decreases. Like the MacArthur and Wilson (1967) model, the disturbance hypothesis predicts that turnover on small islands should be substantial. However, the MacArthur and Wilson (1967) model predicts continuous turnover, whereas the disturbance model predicts synchronous extinctions. A more fundamental difference is that the MacArthur and Wilson (1967) model envisions all communities as being in an ecological equilibrium, whereas the disturbance hypothesis describes small-island communities in a state of disequilibrium.

Evidence for the disturbance hypothesis comes from sessile marine communities, where fouling panels (Osman 1977) or intertidal boulders (McGuinness 1984b) function as islands. Wave action and predation often control diversity in these space-limited systems (Sousa 1984), although the perturbations may not always lead to a species-area relationship. For example, in intertidal boulder fields of California, species richness was greatest on intermediate-sized boulders. Small boulders had low species richness because they were chronically disturbed by wave action. But large boulders also had low species richness because they were rarely overturned and became dominated by a few species of competitively superior algae (Sousa 1979). Thus, even if disturbance frequency is correlated with island area, it may not always lead to a species-area relationship. Biotic “disturbances” may also lead to species-area relationships. In forest bird assemblages, for example, species-area slopes were steeper for guilds that were susceptible to nest predation (Martin 1988), suggesting that this disturbance may be more important in small forest patches. The increased perimeter/area ratio ensures that any “edge effects” will be relatively more severe on small islands.

THE HABITAT DIVERSITY HYPOTHESIS

The habitat diversity hypothesis assumes that species diversity is controlled by the availability of different habitat types. This model predicts that habitat diversity increases with area, and that species richness increases with habitat diversity. Area per se has a minor effect on species richness, and instead serves as a surrogate variable for underlying habitat diversity (Williams 1943).

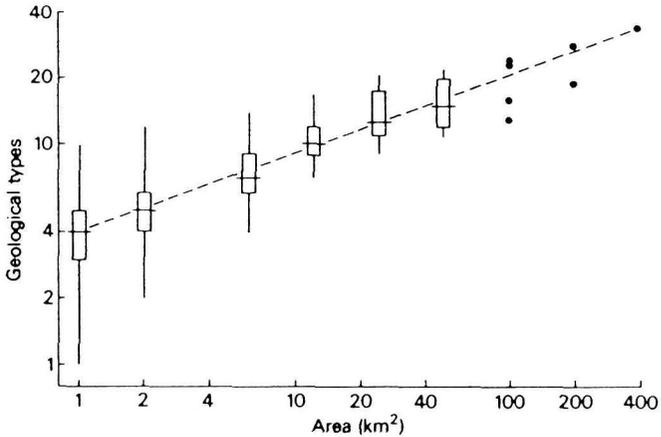


Figure 8.3. Relationship between area and habitat diversity. The x axis is the plot area for regions of England and Wales, and the y axis is the number of geological types recorded in those areas. The box-and-whisker plots illustrate the extremes (vertical lines), quartiles (box ends), and medians (horizontal lines) for multiple observations. The sloping line connects the medians with the total number of geological types observed for the entire area. Note the logarithmic transformation of both axes. The close relationship between area and habitat diversity may be responsible for many species-area relationships. From Williamson (1981), with permission of Oxford University Press.

The habitat diversity hypothesis implies that habitat specialization is important. This explanation fits the naturalist's perspective that many species can be reliably located by paying close attention to their habitat affinities. If unique habitat types are found only on large islands or areas, then species richness will inevitably increase with area. In the West Indian avifauna, for example, single-island endemics such as the Zapata Wren of Cuba (*Ferminia cerverai*) and the Elfin Woods Warbler of Puerto Rico (*Dendroica angelae*) are habitat specialists whose exclusive occurrence on large islands contributes to the species-area relationship.

Several studies have confirmed the basic relationship between habitat diversity and species richness, in both terrestrial (e.g., MacArthur and MacArthur 1961) and marine (e.g., Abele 1974) communities. Much less common are studies of the direct relationship between habitat diversity and area itself. For example the number of geological formations in the Lake District of England was well-correlated with plot area, and the slope of the relationship varied between 0.20 and 0.35 on a log-log scale (Figure 8.3; Williamson 1981). Many

species-area relationships may reflect this underlying pattern of habitat variation and area (Scheuring 1991).

On the other hand, many species are not strict habitat specialists, and species-area relationships are found in very homogeneous habitats, such as mangrove or *Spartina* islands (Wilson and Simberloff 1969; Rey 1981). But even in apparently homogeneous habitats, the perimeter/area ratio will change with island size, and this “edge effect” may represent an important element of habitat diversity (Schoener and Schoener 1981; Janzen 1983). However, without an experimental manipulation, it may be impossible to distinguish the contributions of area and perimeter to species richness (Blouin and Connor 1985).

Multiple Regression Models

How has the habitat diversity hypothesis usually been tested? Historically, habitat and area effects were partitioned with multiple regression analyses (Hamilton et al. 1963; Simpson 1974; Connor and Simberloff 1978). If habitat diversity is important, it should make a statistical contribution to species richness above and beyond the variation explained by area. Although the test is conceptually valid, the tight correlation between area and habitat diversity compromises the statistical analysis. Consequently, the biological interpretation of multiple regressions is problematic, and it has been difficult to tease apart the contributions of area and habitat diversity to species richness (Connor and Simberloff 1978).

For example, bird species richness in isolated woodlots was well correlated with area and vegetation structure (Blake and Karr 1987), but in a multiple regression analysis, only the area effect was statistically significant. However, species richness of interior forest birds was correlated with both area and habitat diversity, whereas richness of edge species was influenced by only area and perimeter. Moreover, habitat diversity was correlated with the abundances of particular species, suggesting that habitat diversity influenced species occurrence and hence total species richness.

Multiple regression analyses can be very sensitive to statistical outliers. For plants of the British Isles, number of soil types contributed significantly to species richness (Johnson and Simberloff 1974), but only if the island of Great Britain was excluded from the analysis (McCoy and Connor 1976). Thus, the measured effects of habitat diversity on species richness may hinge on which groups of species and which groups of islands are considered.

None of these “whole-island” tests is very satisfying. By emphasizing the habitat diversity of an entire island, multiple regression analyses neglect the

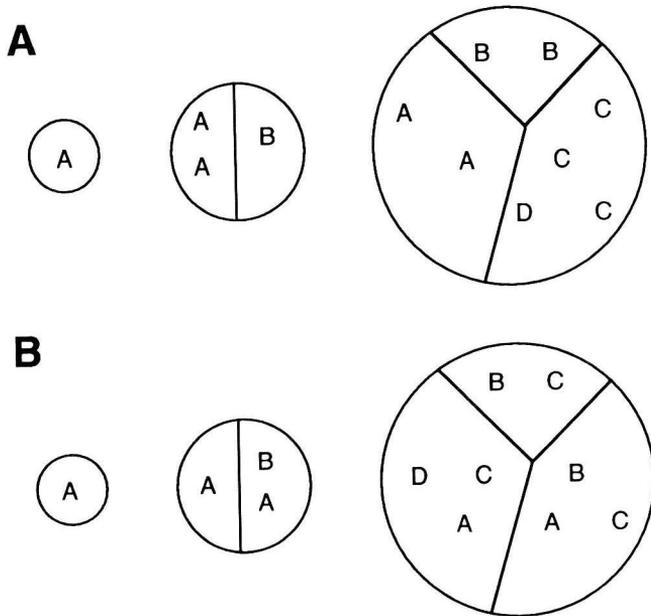


Figure 8.4. Effects of habitat diversity on within-island distributions of species. Each circle is an island, and the divisions within the circle represent different habitat types. The letters represent individuals of different species. In (A), the species-area relationship arises because each species is a specialist on a single habitat type. In (B), habitat diversity does not contribute to the species-area relationship because individuals of the different species occur randomly with respect to habitat type within an island.

spatial patterns of species occurrence *within* islands. If the habitat diversity hypothesis is correct, species will be distributed nonrandomly with respect to different habitats within a single island. In contrast, species may occur randomly within habitats if any of the other three hypotheses is correct (Figure 8.4).

The Habitat Unit Model

This suggests a promising avenue for testing the habitat diversity hypothesis. First, map the habitats of each island, and then record the occurrence of each species within those habitats. If the habitat diversity hypothesis is correct, the relative areas of different habitats should be a better predictor of species richness than total island area.

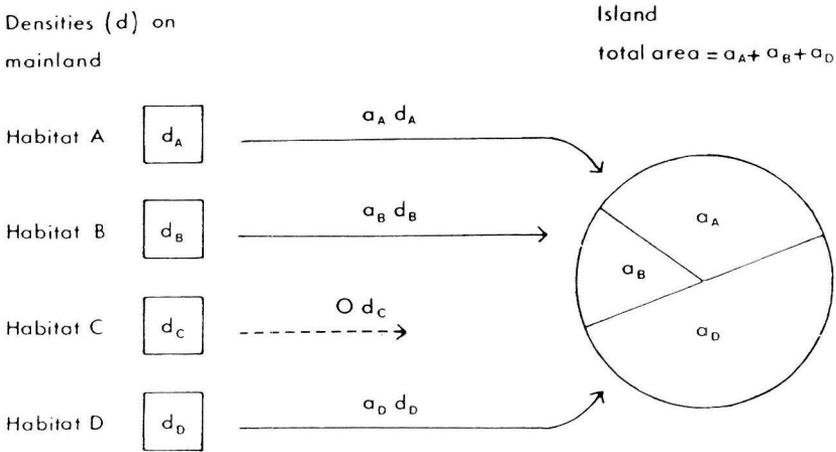


Figure 8.5. Construction of a prevalence function. The density (d) of species in different habitats on the mainland and the relative area (a) of those habitats on the island generate the expected density of each species on an island. From Haila et al. (1983), with permission.

Buckley (1982) took exactly this approach in a study of plant species richness of the Lowendal Islands of Western Australia. For each of 22 islands, Buckley (1982) recorded the distribution of vascular plants in three habitat types: white sand, limestone, and red sand. He next categorized the plant species according to the habitat types in which they occurred. There were three groups of habitat “specialists” that occurred in only one habitat, three groups of species that occurred in exactly two of the habitats, and one group of ubiquitous species that occurred in all three habitats. For a set of n habitats in an archipelago, there will be $2^n - 1$ such groupings or “habitat units.”

For each habitat unit, Buckley (1982) then constructed a species-area curve, using the combined area of the component habitats of each island. Summing the predicted values across all the habitat units gave the expected number of species for an island. This expectation was compared to the predictions from a simple species-area regression that ignored habitats. For 17 of the 22 islands, the predictions of the habitat unit model were superior to those of the simple regression. It is important to note that Buckley’s (1982) result was not a trivial consequence of extreme habitat specialization, because most of the species occurred in two or more habitats.

Haila and Järvinen (1983) took this approach one step further and measured not only the occurrence, but also the abundance, of individual species. Similar

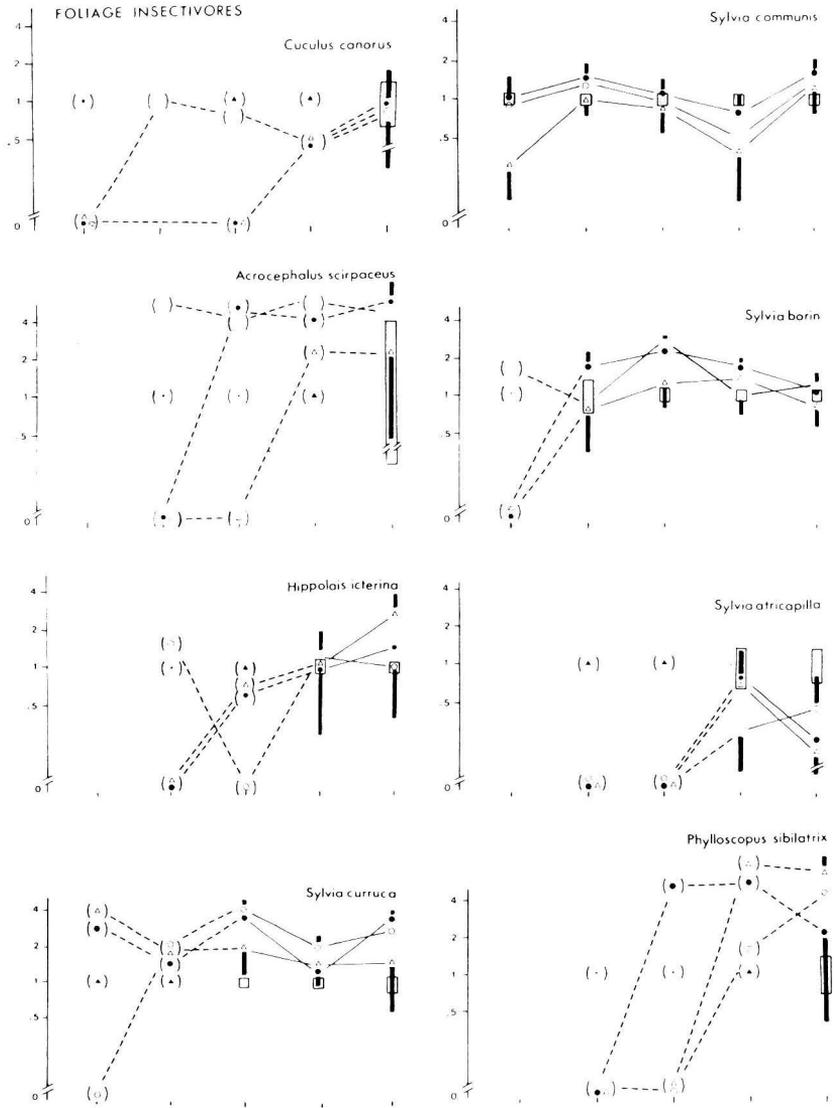


Figure 8.6. Prevalence functions for 8 species of insectivorous birds of the Åland Islands of Finland. Five island size-classes are represented on the x axis. The y axis gives the logarithm of the prevalence function, that is, the ratio of the observed to the expected island density. Symbols indicate data from different yearly censuses. For expectations greater than 5 breeding pairs, the vertical solid line indicates the range and the vertical open bar indicates the standard deviation. Note that for some species the expected density on small islands is effectively zero. From Haila et al. (1983), with permission.

to Diamond's (1975) incidence function (see Chapter 7), the *prevalence function* is the ratio of observed to expected density of a given species on islands of different size (Figure 8.5). For bird species of the Åland Islands of Finland, Haila et al. (1983) constructed the prevalence function by estimating mainland densities of species in different habitats (Figure 8.6). This model accurately predicted species richness, and the authors concluded that a sampling metaphor was appropriate to explain avian species occurrence in this archipelago. Note that the model of Haila et al. (1983) is actually a hybrid of the habitat diversity hypothesis and the passive sampling hypothesis, explained later in this chapter.

In sum, the habitat unit model and the prevalence function are useful tools for evaluating the role of habitat diversity in producing species-area correlations. Because they emphasize the occurrence of species within particular habitats on islands, they are more powerful tests of the habitat diversity hypothesis than conventional regression analyses.

THE EQUILIBRIUM HYPOTHESIS

Popularized by MacArthur and Wilson (1963, 1967) and independently developed by Munroe (1948; see Brown and Lomolino 1989), the equilibrium theory envisions island species richness as a balance between rates of colonization from a mainland source pool of P species and island extinctions of established populations. The theory has two sets of assumptions, one concerning the demography of island populations and the other concerning community-level rates of immigration and extinction. The theory is usually presented in terms of the rate assumptions, but ultimately these are derived from processes at the population level. The population-level assumptions are as follows:

1. The species-abundance distribution of the mainland source pool is a canonical log normal (see Chapter 3). This assumption is not absolutely necessary for the model, but it does generate quantitative predictions about the form and slope of the species-area relationship.
2. The summed abundance of all species is proportional to island area.
3. The probability of population extinction is inversely proportional to island population size.
4. The probability of colonization is inversely proportional to island isolation or distance from the source pool.

The community-level assumptions are:

1. The immigration rate (number of new species/time) decreases with increasing species number on the island and decreases with increasing isolation of the island.
2. The extinction rate (number of species disappearing/time) increases with increasing species number on the island and decreases with increasing island size.

Finally, the predictions that arise from the equilibrium model are:

1. There should be substantial turnover in species composition through time.
2. The species-area curve should be best fit by a power function ($S = CA^z$), where S is species richness, A is island area, and C and z are fitted constants.
3. The slope of the curve on a log-log plot (z) should approximate 0.26 for isolated archipelagoes, and should be shallower with decreasing isolation.
4. Species number on an island should be relatively constant through time, although some variability in S is expected because extinctions and recolonizations are stochastic (Diamond and May 1977).
5. In a comparison of equal-sized quadrats, species density should be higher on the mainland or on large islands than on small islands.

TESTS OF THE ASSUMPTIONS

In the following sections, we review the evidence supporting the important assumptions and predictions of the equilibrium theory. Some, but not all, of these patterns have been tested with null models.

Do Extinction and Immigration Rates Vary with Species Number?

Graphs of extinction and immigration rates as a function of species number are the most famous summary of the MacArthur and Wilson (1967) model. The precise shape of these curves depends on species interactions and immigration dynamics. If species extinctions are independent (a noninteractive community)

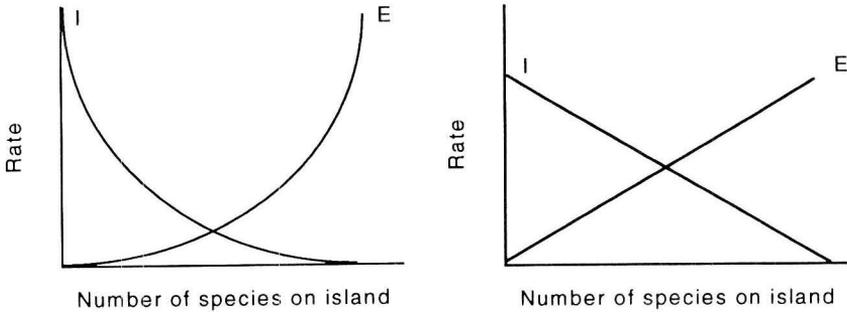


Figure 8.7. Concave and linear immigration (I) and extinction (E) curves. The original MacArthur and Wilson (1963) model presented concave immigration and extinction curves, whereas a Markovian model generates linear curves.

and species immigrations are equiprobable, the curves are strictly linear. In contrast, an interactive or heterogeneous assemblage will give concave immigration and extinction curves (MacArthur 1972), which is how the theory was originally presented (Figure 8.7). This distinction is important for null model tests of species constancy, which we describe later in this chapter. However, for a qualitative test of the MacArthur and Wilson (1967) model, it is sufficient to show that the immigration rate falls and the extinction rate rises with increasing island species richness.

In spite of the obvious importance of the immigration and extinction curves to the equilibrium theory, long-term sampling data are necessary to construct them, and there are few examples from the literature. Strong and Rey (1982) demonstrated a significant increase in extinction rate and a significant decrease in immigration rate for insect recolonization of fumigated *Spartina* islands (Rey 1981). Williamson (1981) assembled three other examples from long-term census data in insular assemblages. For an established bird community in Eastern Wood, Williamson (1981) plotted extinction and immigration rates as a function of species number for 26 yearly censuses. Immigration rates declined significantly with S , but extinction rates did not increase significantly (Figure 8.8). For birds of Skokholm Island, only the extinction rate was significantly correlated with island species richness. The correlation for the immigration curve was nonsignificant and had a positive, not a negative, slope.

Williamson's (1981) final example was plant colonization data for the volcanic island of Surtsey. In this study, the highest immigration rates occurred not at the start of colonization, but after some initial pioneer species became established, perhaps indicating successional changes in the hospitability of the island. In all of these examples, the variance about the curves was substantial,

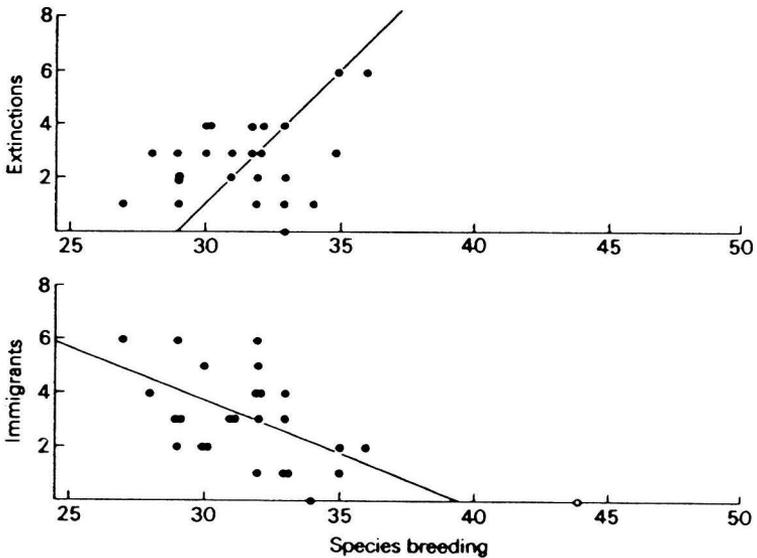


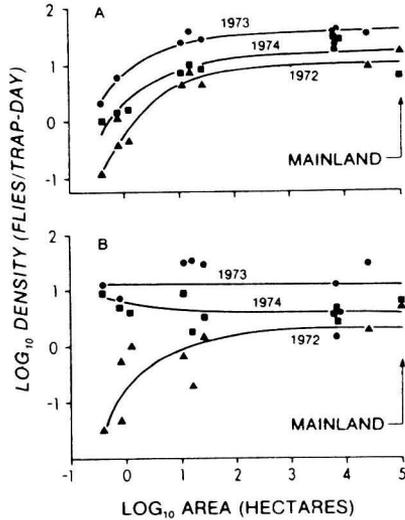
Figure 8.8. Immigration and extinction curves for breeding birds of Eastern Wood. The immigration curve decreases significantly with increasing S , as predicted by the MacArthur and Wilson (1967) model, but the increase in the extinction rate is not significant. Compare with Figure 8.7. From Williamson (1981), with permission of Oxford University Press.

suggesting that species number had only a very minor effect on local immigration and extinction rates.

Do Population Sizes Vary with Island Area?

In spite of the critical importance of population size and stochastic extinction to the MacArthur and Wilson (1967) theory, relatively few studies have examined how total population size of an individual species changes as a function of island area (Haila and Järvinen 1981). One problem is that MacArthur and Wilson (1967) were not entirely explicit about what the predicted patterns were. As developed by Schoener (1976b), there are two possibilities. The first is that the fauna is noninteractive and population size is proportional to area. In the second model, competition is proportional to species number, so that average population size is a function of both island area and species richness. Whether or not the fauna is interactive, it would seem that a basic prediction of the MacArthur and Wilson (1967) model is that equilibrium population sizes increase with island area (Preston 1962).

Figure 8.9. Average population densities of *Drosophila* species as a function of island area. (A) *D. affinis* subgroup species. (B) Mushroom-feeding species. Curves are fit to data collected in three different years. Mainland densities are shown on the far right. From Jaenike, J. 1978. Effect of island area on *Drosophila* population densities. *Oecologia* 36:327–332, Figure 1. Copyright © 1978 by Springer-Verlag GmbH & Co. KG.



Jaenike (1978) measured *Drosophila* densities on islands off the coast of Maine (Figure 8.9). For the *D. affinis* subgroup, density was constant for large islands and mainland areas, but dropped off sharply for small islands. Thus, populations on small islands were even smaller than would be predicted on the basis of area alone. On small islands, exposure to wind and violent storms may have depressed population densities, which were correlated with the ratio of island circumference to area. For mushroom-feeding *Drosophila*, the relationship between island area and density was less clear-cut and varied among years, perhaps because these populations tracked fluctuations in mushroom density. Jaenike's (1978) results suggest that the relationship between population size and island area may not be linear, and that the factors that regulate species richness may be fundamentally different on large than on small islands.

Also working in the Deer Island Archipelago in Maine, Crowell (1973, 1983) introduced deer mice and voles onto rodent-free islands. These island populations grew to greatly exceed mainland population densities, which were probably limited by predation and dispersal. For islands in the Gulf of California, the highest densities of the lizards *Uta* and *Cnemidophorus* were found on small islands (Case 1975). Contrary to the assumptions of the MacArthur and Wilson (1967) model, lizard density declined with increasing species richness and island area.

These examples cast doubt on one of the basic premises of the equilibrium model—that population size is proportional to island area. Although the idea that N increases with area is intuitively reasonable, the frequent occurrence of

density compensation (MacArthur et al. 1972; Wright 1980), habitat shifts (Ricklefs and Cox 1978; Crowell 1983), and ecological release from predators and competitors (Toft and Schoener 1983) suggests that island area is not always the overriding factor that determines insular population size.

TESTS OF THE PREDICTIONS

Is There Substantial Turnover in Species Composition?

Turnover is one of the most salient features of MacArthur and Wilson (1967) equilibrium communities. It distinguishes the MacArthur and Wilson (1967) model from other scenarios of insular community assembly, including co-evolutionary models of species interaction (see Chapters 6 and 7) and non-interactive colonization models with little or no turnover (Case and Cody 1987). Unfortunately, turnover in island populations may be difficult to establish. Measures of turnover are affected by the thoroughness of sampling effort at different times (Lynch and Johnson 1974), the length of the census interval (Diamond and May 1977), sampling error (Nilsson and Nilsson 1983), the establishment of a species equilibrium (McCoy 1982), the occurrence of habitat change between censuses (D.L. Lack 1976), and the use of relative versus absolute turnover rates (Schoener 1988b).

More importantly, the measurement of turnover depends critically on how an investigator defines colonization, extinction, and residency status. If vagrant or nonresident species are included in the calculations, estimates of turnover can be greatly inflated. For example, Simberloff and Wilson (1969) initially estimated turnover rates of insect species colonizing mangrove islands at 0.67 species per island per day. Simberloff (1976a) reanalyzed the data and eliminated probable transients and widely dispersing species. The revised turnover estimate was only 1.5 species per island per year! Similarly, Whitcomb et al. (1977) computed turnover rates for forest birds of 15–25% over 30 years. But if edge species and wide-ranging raptors were excluded, the turnover was close to 0 (McCoy 1982). Williamson (1989) concluded that the MacArthur and Wilson (1967) model is thus “true, but trivial.” In other words, many communities do display substantial turnover, but this inevitably occurs among transient, peripheral species that may not be typical residents of the community.

However, not all “transient” turnover is biologically uninteresting. It is important to distinguish between turnover of populations and turnover of individuals through movement among sites. In some cases, community assembly occurs through individual movement. For example, breeding birds of

coniferous forest seasonally colonize habitat fragments and establish breeding territories (Haila et al. 1993), so that turnover does not reflect true population extinction. Haila et al. (1993) suggested that seasonal movement of individuals is likely to be very important in the structure of many boreal animal communities.

Is the Species-Area Curve Best Fit by a Power Function?

The log normal distribution provided a theoretical justification for using the power function in species-area studies (Preston 1962). But if the species abundance distribution is not log normal, other transformations may be more appropriate. For example, if a log series describes abundances, an exponential (semi-log) transformation will linearize the species-area relationship (Fisher et al. 1943; Williams 1943, 1947b). McGuinness (1984a) reviewed the extensive history of efforts by plant ecologists to infer the correct functional form of the species-area relationship. For animal ecologists, the power function quickly became synonymous with the log normal distribution (Preston 1960, 1962) and the equilibrium model (MacArthur and Wilson 1967). However, Coleman et al. (1982) warned that inferring the species abundance distribution from the species-area transformation requires that the same distribution hold for all islands in an archipelago, which is a tenuous assumption.

What is the empirical evidence that the power function or the exponential provides the best fit to species-area data? Connor and McCoy (1979) fit regression models to a heterogeneous collection of 100 species-area curves from the literature. Using logarithmic and untransformed data, they chose the best-fitting model as the one that linearized the curve and minimized least-squares deviations (high r^2). In some cases, more than one model fit the data equally well (r^2 values differed by less than 5%). These criteria were somewhat arbitrary (Sugihara 1981), but without repeated measurements of species richness on islands of identical size, there seems to be no other reasonable way to assess the fit of a regression model (Connor et al. 1983).

Although the power function (log-log model) fit three-quarters of the data sets, it was the best-fitting model in only 43 of 119 cases. The exponential model did not fare any better, and in many cases, the untransformed data gave the best fit. Unless the assumptions of the MacArthur and Wilson (1967) model can be confirmed independently, there seems to be little biological significance to the transformation that best linearizes a species-area curve.

What Is the Observed Value of z , and What Is Its Significance?

Although the log-log transformation may have little biological significance, there is a long tradition of interpreting the slope of this regression in the context of equilibrium theory. The impetus came from Preston (1962), who derived a slope of 0.26 for an archipelago of “isolates” sampled from a log normal distribution. He felt that sampling errors and other factors would lead to slope values in the range of 0.17 to 0.33, whereas MacArthur and Wilson (1967) accepted a range of 0.20 to 0.35. May (1975a) derived slopes in the range of 0.15 to 0.39 for a variety of log normal distributions, and Schoener (1976b) predicted slopes between 0 and 0.5 for an equilibrium model with species interactions.

Within the equilibrium framework, species-area slopes were thought to reflect the degree of isolation of an archipelago. In the original MacArthur and Wilson (1967) model, isolation affected only the immigration curve, so that distant islands had lower species richness and distant archipelagoes had steeper slopes. Lomolino (1984) confirmed this pattern for mammals in island archipelagoes: the slope of the species-area relationship was correlated with the relative isolation of an archipelago (Figure 8.10).

However, isolation may affect the extinction rate as well (Brown and Kodric-Brown 1977), making it unclear what slope ought to be expected. Schoener (1976b) thought that distant archipelagoes would be colonized primarily via a

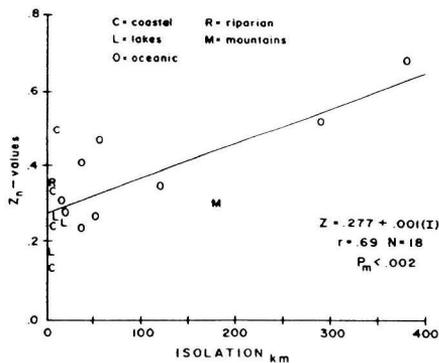


Figure 8.10. Effects of isolation (average distance to the nearest mainland or large island) on the slope of the species-area regression. Each symbol represents a different archipelago. As the original MacArthur and Wilson (1967) model predicted, slopes were steeper for more isolated archipelagoes. From Lomolino, M. V. 1984. Mammalian island biogeography: effects of area, isolation and vagility. *Oecologia* 61:376–382, Figure 2. Copyright © 1984 by Springer-Verlag GmbH & Co. KG.

“stepping stone” effect from other occupied islands, rather than from a distant source pool. In addition, the pool of species for a distant archipelago may be smaller than for a close archipelago. In Schoener’s (1976b) models, these effects generated shallower slopes for distant archipelagoes, a pattern that holds for some avian species-area data. These extensions of the MacArthur and Wilson (1967) model suggest that a wide range of slopes are possible for equilibrium communities.

Slopes of species-area curves have also been used to compare taxa within an archipelago. A shallow species-area slope for a taxonomic group has often been interpreted as an indicator of good colonization potential (Terborgh 1973a; Faaborg 1979): because successful colonizers can reach many islands in an archipelago, the increase in species richness due to area is much weaker than for a group of poor dispersers.

But before species-area slopes can be interpreted in the context of equilibrium theory, other forces that affect z must be considered. First, there are a number of statistical decisions that affect the slope of the species-area curve (Loehle 1990b). For example, the estimate of the slope will depend on whether the power function or the linear log-log model is fit. The two models are not equivalent; they treat the error term differently and may give different slope estimates (Wright 1981). The slope of the curve may also be affected by the range of island sizes considered. If the range of areas sampled is too narrow, the area effect may not be statistically significant (Dunn and Loehle 1988). Slopes also tend to be much steeper for archipelagoes of small islands than large islands (Martin 1981). Finally, slope estimates may be sensitive to the particular islands included in the sample. For example, the estimated species-area slope for butterflies of woodland lots (Shreeve and Mason 1980) is 0.28 ($n = 22$ lots), but z ranges from 0.23 to 0.35, following the deletion of a single island from the sample (Boecklen and Gotelli 1984). This sort of statistical variation suggests that differences in slope will have to be substantial to reflect any biological meaning.

For these reasons, comparisons of slope among different taxonomic groups are problematic. For Neotropical birds, species-area slopes varied markedly among different families (Terborgh 1973a; Faaborg 1979). However, most of this variation in slope could be attributed to variation in species richness within families (Gotelli and Abele 1982). Regardless of dispersal potential, families with very few species will have shallow species-area slopes (Figure 8.11). The estimated slope in a regression is also proportional to the correlation coefficient. Grafen (1984) showed similar effects of species richness on the comparison of r^2 values among guilds of insects associated with British trees (Kennedy and Southwood 1984).

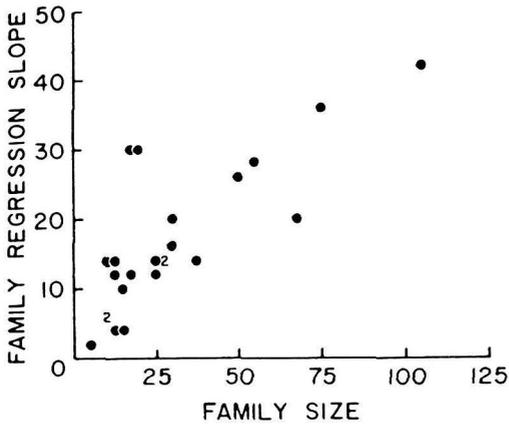


Figure 8.11. Effects of species richness on the slope of the species-area regression. Each point is a different family of West Indian land birds. From Gotelli and Abele (1982), with permission.

In addition to these important statistical considerations, slopes of species-area curves will be influenced by biological forces that are not explicitly considered in the equilibrium model. For example, habitat diversity will affect the slope as different species sets are added with new habitat types on large islands (Williams 1943). From published studies of forest plots in the eastern United States, Boecklen (1986) quantified habitat diversity with a principal components analysis of vegetation measures, and then randomly combined plots of differing size and habitat diversity. Species-area curves for breeding birds were steeper for “archipelagoes” with strong habitat heterogeneity.

Incidence functions and minimal area requirements of particular species can also generate a range of slope values that span the interval suggested by the equilibrium hypothesis (Abbott 1983). Disturbance (McGuinness 1984a) and predation (Martin 1988) may also change the slope of the curve. Finally, species-area curves may change during the course of colonization (Schoener and Schoener 1981), although for vascular plants on lake islands in Sweden, the slope did not change during a century of primary succession (Rydin and Borgegård 1988).

Given all these factors, it is not surprising that Connor and McCoy’s (1979) literature survey yielded a wide range of slope values, of which only 55% fell within the liberal range suggested by MacArthur and Wilson (Abbott 1983). Connor and McCoy (1979) suggested that any tendency for slope values to cluster between 0.2 and 0.4 was an artifact. They argued that the pattern was generated by the small variance in species number relative to variance in island area, and by the fact that small or nonsignificant correlation coefficients would be underrepresented in the literature. Because the estimated slope in a regression is the product of the correlation coefficient and the ratio of variances of y to x , it follows that slopes in this range are often expected by chance.

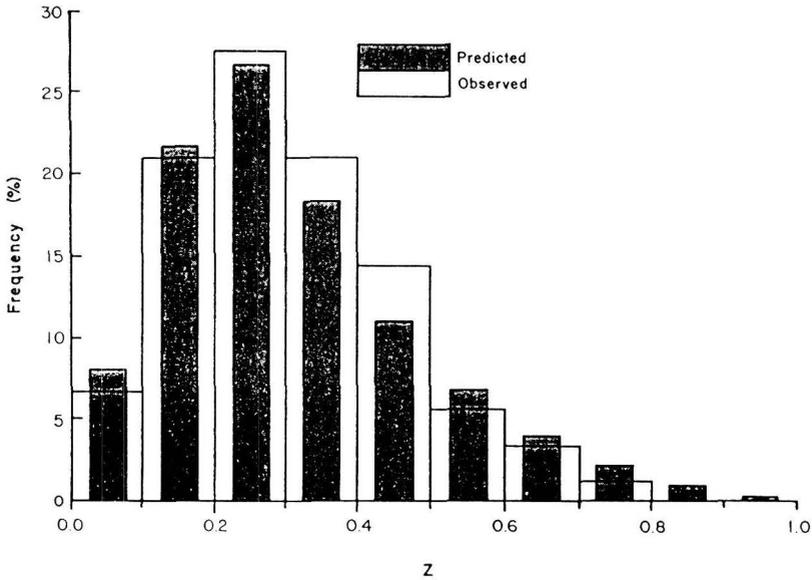


Figure 8.12. Distribution of 100 species-area slopes. Although most observed values fall between 0.20 and 0.30, this pattern is predicted by the observed variances in area and species richness and by the observed distribution of correlation coefficients. Reprinted by permission of the publisher from Connor, E. F., E. D. McCoy, and B. J. Cosby. 1983. Model discrimination and expected slope values in species-area studies. *American Naturalist* 122:789–796. Copyright © 1983 by The University of Chicago.

Sugihara (1981) argued that this analysis was incorrect and that observed slopes were significantly clustered in a narrow range. However, a reanalysis using observed variances and marginal distributions of r confirmed that there was no tendency for slopes to cluster (Figure 8.12). For carefully selected archipelagoes, it may be possible to interpret relative values of z (Martin 1981). But the most sensible view is that slopes of species-area curves are simply fitted constants, with little or no biological significance (Connor and McCoy 1979; Gilbert 1980; Abbott 1983).

Less attention has been given to the intercept of the species-area relationship (Gould 1979), although the statistical problems will be similar to those of slope analyses. Nevertheless, if the slopes of two species-area curves are identical, the intercept represents the expected species richness after controlling for differences in area. For example, Abele (1976) compared species richness of decapod crustaceans inhabiting coral heads in constant and fluctuating environments. Although there was a significant species-area relationship, the intercept

was higher for coral heads in the fluctuating environment, indicating greater local species richness. Note that a comparison of intercepts statistically removes the effect of area from the comparison of species richness.

The initial appeal of the equilibrium theory motivated much research in biogeography (Brown 1981), but the interpretation of species-area slopes has been a largely unproductive avenue. There are some communities that seem to fit the MacArthur and Wilson (1967) model (e.g., Rey 1981), but the critical tests come from observations of turnover and population extinctions on islands, not from statistical curve fitting. Like the Hutchinsonian size ratio of 1.3 (see Chapter 6), the z value of 0.26 is another of ecology's "magic numbers" that has not withstood detailed scrutiny.

Is Species Number Constant Through Time?

Although the MacArthur and Wilson (1967) model describes a steady-state balance between immigration and extinction, it does not predict a strict constancy in S through time, because immigration and extinction curves reflect underlying probabilities of discrete events (Diamond and Gilpin 1980). The intersection of the immigration and extinction curves yields the expected species number with an associated variance.

But how much variability is acceptable? In other words, how much change is expected in species number at equilibrium for the MacArthur and Wilson (1967) model? Keough and Butler (1983) noted that many ad hoc limits have been invoked in the literature; authors have claimed a species equilibrium for temporal coefficients of variation (CV) between 5 and 75%. Using literature data and computer simulations of different sampling distributions, Keough and Butler (1983) suggested a rough empirical limit of approximately 10%. Comparison with any cutpoint is dependent on sample size, and Keough and Butler (1983) provided statistical tests for deciding whether the CV is greater or less than some hypothesized value. Applying the "10% rule" to their own data on marine epifauna of mollusc shells, they rejected the null hypothesis—temporal fluctuations in S were too large to be considered in equilibrium. Much of the variability in S was due to chance colonization of shells by colonial ascidians, which were superior space competitors. Predation by monocanthid fishes removed these ascidians and greatly reduced the variability.

Even with such an empirical guide, documentation of equilibrium is tricky. Species number on real or virtual islands is always bounded between 0 and P , the species pool size, so the fact that a mean and a variance can be calculated for a series of census data need not imply an underlying equilibrium (Boecklen and Nosedal 1991). Instead, an explicit null model for temporal change in

species richness should be used. If a real community is in equilibrium, temporal fluctuations in S should be substantially smaller than predicted by the null model.

Simberloff (1983c) used a Markov model of species colonization and extinction to contrast with the MacArthur and Wilson (1967) equilibrium model. For each species k in the source pool, the Markov model assumes a constant probability of successful immigration during a given time period (i_k) and a constant probability of extinction (e_k). The corresponding probabilities of not immigrating and not going extinct are $(1 - i_k)$ and $(1 - e_k)$, respectively. These probabilities need not be equivalent for all species. If species immigrations and extinctions are independent of one another, an equilibrium will be reached at

$$\hat{S} = \sum_{k=1}^p \frac{i_k}{i_k + e_k} \quad (8.1)$$

This noninteractive Markov model has been derived many times, for both island biogeography models (Bossert 1968; Simberloff 1969; Gilpin and Diamond 1981) and analogous single-species metapopulation models (Gotelli 1991). The Markov model generates linear immigration and extinction curves, in contrast to the concave curves of the MacArthur and Wilson (1967) model. Both models predict an equilibrium determined by the balance between immigration and extinction, and both models predict that species number will decline if it is above that equilibrium.

However, the forces leading to this decline are somewhat different for the two models. In the Markov model, species richness declines above equilibrium, because it is improbable that such a large number of species will persist through time. Extinctions will outnumber colonizations and S will decline. Demographic factors are not invoked in these extinctions. In the MacArthur and Wilson (1967) model, an increase in S implies a decline in the population size of each component species, because of an assumed limit on summed population densities. With smaller population sizes, the probability of extinction increases and species number declines. In the MacArthur and Wilson (1967) model, the immigration and extinction curves are more divergent than in the Markov model, so that species number will return more rapidly if it is displaced either above or below equilibrium. The steeper the curves and the greater their concavity, the faster the return to equilibrium (Figure 8.13; Diamond and Gilpin 1980).

Thus, in a regulated MacArthur and Wilson (1967) equilibrium, variance or change in S should be smaller than under the null hypothesis of the Markov model. Simberloff (1983c) fit the Markov model to bird census data from

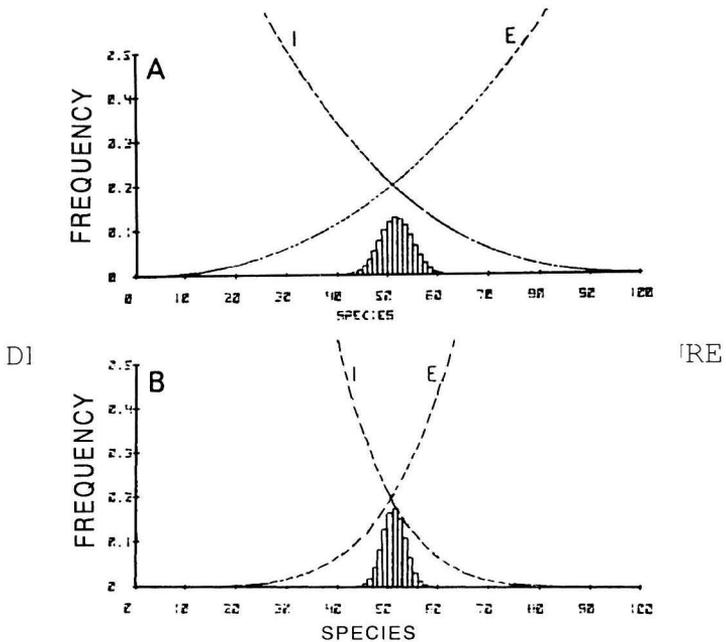


Figure 8.13. Effects of immigration (I) and extinction (E) curves on frequency distribution of species number (S) at equilibrium. The steeper and more concave the immigration and extinction curves, the less variability in S at equilibrium. Reprinted by permission of the publisher from Diamond, J. M., and M. E. Gilpin. 1980. Turnover noise: contribution to variance in species number and prediction from immigration and extinction curves. *American Naturalist* 115:884–889. Copyright © 1980 by The University of Chicago.

Skokholm Island and the Farn Islands, and the forested plot of Eastern Wood (Figure 8.14). Because independent estimates of extinction and immigration probabilities were not available, Simberloff (1983c) estimated them from the sequential census data. Using the Markov transition probabilities, Simberloff (1983c) generated a null distribution by simulating each species trajectory, starting with the island composition observed in the initial census.

The null hypothesis was never rejected in the direction of the regulated equilibrium, and observed measures of variance in S were usually in the wrong tail of the distribution. For the Skokholm data, the variance was significantly greater than even that predicted by the Markov model. This result is consistent with Williamson's (1981) finding that the immigration curve for these data showed a nonsignificant increase with species richness. With the immigration and extinction curves both increasing with S , fluctuations in species number

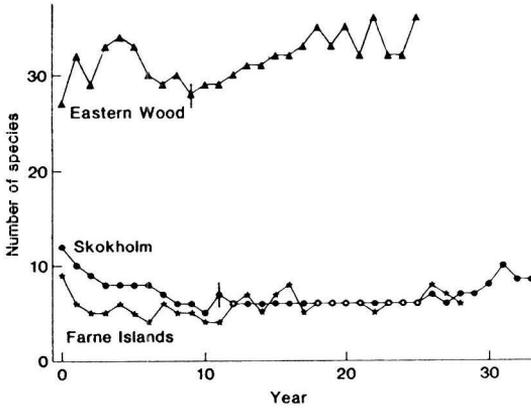


Figure 8.14. Species trajectories for birds of Skokholm Island and Farne Islands and Eastern Wood. Vertical lines indicate years in which more than one census was conducted. These trajectories could not usually be distinguished from those generated by a noninteractive Markovian model (see Figure 8.7). Reprinted with permission from Simberloff, D. 1983. When is an island community in equilibrium? *Science* 220:1275–1277. Copyright © 1983 American Association for the Advancement of Science.

will be especially large. Simberloff (1983c) concluded there was little evidence from these analyses to support a model of regulated species equilibrium.

Simberloff's (1983c) analysis was predicated on the idea that the observed sequence of presences and absences provided a reasonable empirical estimate of extinction and immigration probabilities. Boecklen and Nosedal (1991) explored this problem with seven species trajectories drawn from the literature. They assumed that the estimated transition probabilities were true and simulated 30 new presence-absence matrices for each set of trajectories. Transition probabilities were again estimated from each new matrix, and 1000 additional species trajectories were generated. Finally, the 30 estimates of cumulative probabilities were compared to the probability value estimated from the original presence-absence matrix. If estimates of transition probabilities from the original matrix were valid, they should have been equivalent to those that were secondarily estimated from the new presence-absence matrices.

However, the original and derived probability estimates usually did not agree. Sometimes the observed probability values were too conservative, and sometimes they were overly liberal; results varied unpredictably among data sets. This analysis also showed that coefficients of variation, even if tested statistically by the Keough and Butler (1983) method, were unreliable indicators of equilibrium status. Boecklen and Nosedal (1991) concluded that al-

though the Markov model was probably valid for testing equilibrium status, transition probabilities should not be estimated from the same data set to be tested. A reanalysis using maximum likelihood estimates (Clark and Rosenzweig 1994) would be informative, because the transition probabilities estimated by Simberloff (1983c) and by Boecklen and Nosedal (1991) may be biased in some cases.

Does Species Richness Increase in Equal-Sized Quadrats?

An important prediction from Preston's (1962) work has been relatively neglected in the species-area literature: in an equilibrium community, not only will total species richness be greater on the mainland than on islands, but so will species richness in *equal-sized* quadrats. This is because the mainland supports many rare species from the tail of the log normal distribution that would not occur on islands. A similar logic can be applied to a comparison of large and small islands. If the MacArthur and Wilson (1967) model is correct, there should be a significant correlation between S and island area for equal-sized quadrats sampled *within* islands.

Westman (1983) first tested this hypothesis in xeric shrublands of the California Channel Islands. Although there was a significant overall species-area relationship, the number of plant species per quadrat showed no relationship with island area. Kelly et al. (1989) found only a weak positive correlation between island area and local richness of plants for islands in Lake Manapouri, New Zealand. Island area accounted for no more than 17% of the variance in species number in equal-sized quadrats, whereas area accounted for 92% of the variation in whole-island species richness (Quinn et al. 1987).

For animal communities, Stevens (1986) examined the species-area relationship for wood-boring insects and their host plants by sampling insect communities at different sites within the geographic range of the host. Although species richness of insects was correlated with the size of the geographic range of the host species (the measurement of "area"), richness within sites did not show a significant host-area effect. All these studies point to the fact that species were not uniformly distributed within an island. The results suggest that total island area (or host geographic range size) did not have a direct effect on local population size and hence on total species richness.

THE PASSIVE SAMPLING HYPOTHESIS

Biological processes such as local extinction, chronic disturbance, and habitat specialization have provided competing explanations for the species-area rela-

tionship. But the correlation could also arise as purely a sampling phenomenon. The passive sampling hypothesis (Connor and McCoy 1979) envisions individuals as “darts” and islands as “targets” of different area. Continuing this analogy, different colors of darts represent the different species, and the darts are tossed randomly at the array of targets. It follows that large islands will accumulate more darts, and hence more species, than will small islands.

Arrhenius (1921) introduced this model and found good agreement between observed and predicted species richness for plants in quadrats of different size. However, the passive sampling hypothesis was largely ignored in the species-area literature until Coleman (1981; Coleman et al. 1982) developed the theory mathematically.

The passive sampling hypothesis has only two assumptions:

1. The probability that an individual or a species occurs on an island is proportional to island area.
2. Islands sample individuals randomly and independently. In other words, inter- or intraspecific forces do not modify the probability of individual occurrence.

Given these assumptions, the passive sampling hypothesis predicts the expected species richness for an island as

$$E(S_j) = \sum_{i=1}^S 1 - \left(1 - \frac{a_j}{A_T}\right)^{n_i} \quad (8.2)$$

where a_j is the area of the j th island, A_T is the summed area of all islands, and n_i is the abundance of species i summed over all islands. The term inside the summation sign is the probability that species i occurs on the island, given n_i dart tosses at the target. When summed across all species, this gives the expected species number.

Coleman (1981) also derived the variance of species richness and the expected slope of the species-area curve, which could be compared to values derived from equilibrium theory or other hypotheses. However, Coleman's (1981) slope test may not always discriminate among different hypotheses (McGuinness 1984a). Because the expected slope is ultimately determined by the species abundance distribution, a range of curves is possible. The extremes are a linear species-area relationship for an inequitable species abundance distribution and a steep, monotonic curve for a perfectly equitable assemblage (Figure 8.15). Exponential or power function curves may lie between these two extremes (McGuinness 1984a). These curves are identical in shape to those

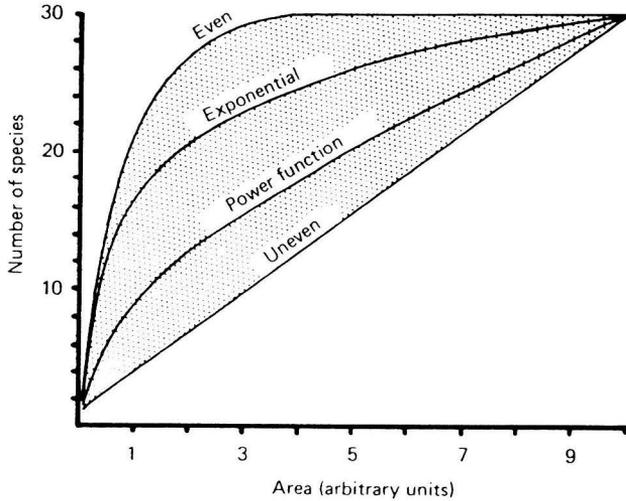


Figure 8.15. Effect of the underlying species abundance distribution on species richness in the passive sampling model. The exponential and power functions will often lie between the extremes generated by a maximally even or uneven species abundance distribution. Compare with Figure 2.7. From McGuinness (1984a). Reprinted with the permission of Cambridge University Press.

generated by rarefaction (see Figure 2.7 in Chapter 2) because each island effectively rarefies the collection to a small sample determined by relative island area.

The passive sampling hypothesis is appealing as a null model because of its simplicity—the observed collection of individuals in the archipelago is taken as the possible universe from which samples (island communities) are randomly drawn. As in the MacArthur and Wilson (1967) model, species richness in the passive sampling model depends on the species abundance distribution. However, the MacArthur and Wilson (1967) model envisions extinctions due to small population size as the ultimate cause of the species-area relationship, whereas the passive sampling hypothesis makes no demographic assumptions. Instead, areas function only as targets that randomly accumulate individuals and species. The idea that island immigration is proportional to island area seems biologically reasonable. In contrast, the equilibrium theory assumes that area controls only the extinction process (Brown and Kodric-Brown 1977). The best independent evidence for the “target-area” effect on immigration is that migration of mammals across ice onto islands in the St. Lawrence River was correlated with island area (Lomolino 1990).

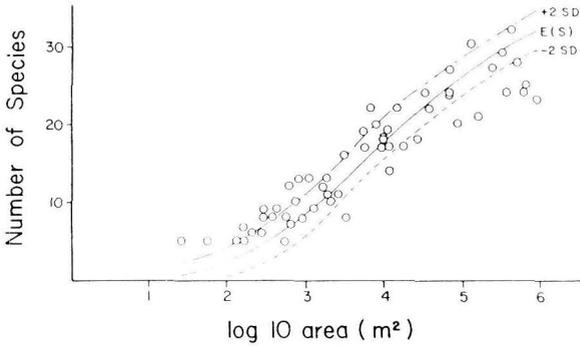


Figure 8.16. Observed and expected plant species richness (legumes, milkweeds, and goldenrods) for prairie remnants. The solid line is the expected value based on a passive sampling model adapted for presence-absence data. Reprinted from Simberloff, D., and N. Gotelli. 1984. Effects of insularisation on plant species richness in the prairie-forest ecotone. *Biological Conservation* 29:27–46, p. 35. Copyright © 1984, with kind permission from Elsevier Science Ltd, The Boulevard, Langford Lane, Kidlington OX5 1GB, UK.

One disadvantage of the passive sampling hypothesis is that it requires measurements of island population sizes. Because these data are difficult to obtain, there have been relatively few tests of the passive sampling hypothesis. If abundance data are not available, an analogous test can be conducted with presence-absence data. Observed species occurrences are reshuffled randomly among islands, with probabilities of occurrence proportional to island areas. Simberloff and Gotelli (1984) used this method to predict plant species richness in prairie and forest remnants. The observed and expected species richness showed reasonable agreement, although richness was somewhat higher than expected for very small patches and lower than expected for large patches (Figure 8.16).

When data are available on the distribution of individuals, the passive sampling hypothesis has proven useful as a baseline for examining species-area curves. The hypothesis adequately explained over half of the species-area curves for sessile organisms of rocky intertidal boulders in Australia (McGuinness 1984b). For breeding birds on islands in a Pennsylvania reservoir, the passive sampling hypothesis provided a better fit to species-area data than did a power or exponential function (Figure 8.17). At a larger spatial scale, passive sampling characterized most species-area relationships for vascular plants of the Appalachian Mountains and provided a method for estimating the number of rare species to be found in a region (Miller and Wiegert 1989).

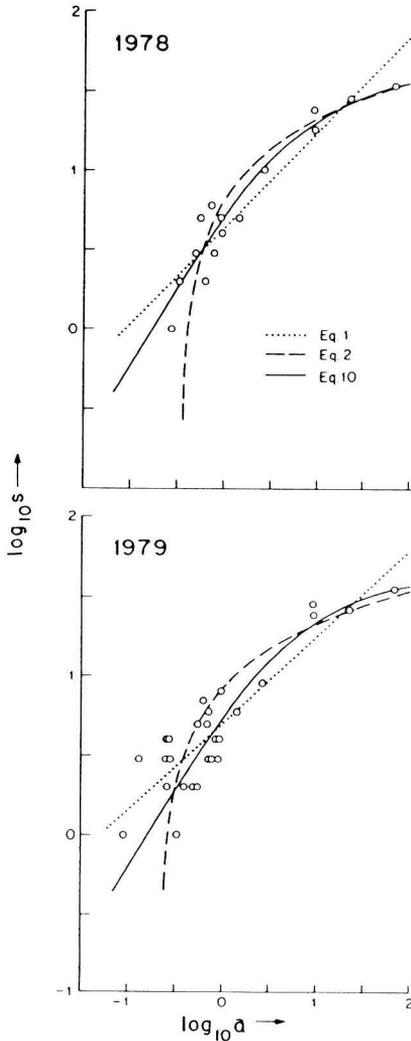


Figure 8.17. Fit of the exponential function, power function, and passive sampling model to species-area data. The x axis is the logarithm of island area, expressed as a proportion of the total area of the archipelago. The y axis is the logarithm of island species number. Each point is the observed number of breeding bird species on forest islands in Pymatuning Lake for census data in two consecutive years. The straight line is the power function, the dashed curve is the exponential function, and the solid curve is the expectation from the passive sampling model. Exponential and power functions were fit by standard linear regression. Note the superior fit of the passive sampling model to observed data. From Coleman et al. (1982), with permission.

In other communities, however, the passive sampling model overestimates species richness. For example, Gotelli et al. (1987) tested the model for an amphipod-mollusc assemblage that colonized artificial substrates in the Gulf of Mexico. Observed species richness was less than expected, and the deviations became more severe as colonization proceeded, perhaps due to crowding in a space-limited habitat. For natural rock islands, Rytí (1984) also found that the species richness of perennial plants was less than predicted by the passive

sampling model. He suggested that multiple source pools and dispersal constraints might account for the discrepancy.

If the assumption of independent placement of individuals is violated, then the summed abundance of a species (n_i) will not provide an accurate estimate of the probability of occurrence (Abele and Patton 1976). For example, if density compensation leads to large population sizes on a few islands, the passive sampling hypothesis will simulate the random placement of those individuals across many islands and therefore lead to an overestimate of species richness for most islands. In the analysis of species co-occurrence patterns (Chapter 7), it was necessary to control for differences in species richness among islands. Conversely, in the analysis of species richness, it may be necessary to control for species interactions and demographic limits on island population sizes.

A more subtle problem is that the passive sampling model provides only a “snapshot” explanation for the species-area curve. For habitats that are recolonized seasonally (Osman 1977; Haila 1983), the system is periodically reset and the passive sampling model can be applied to colonization within a single season. But suppose there is a stable mainland pool of species, such that immigrants are continuously available for island colonization. In other words, there is an unlimited supply of “darts” that can be tossed at the target. If passive sampling continues over a long period of time, we would expect small islands to eventually accumulate the same set of species as large islands. The passive sampling hypothesis does not address the accumulation of species on small islands through time. In contrast, the other three hypotheses for the species-area relationship invoke some mechanism that ultimately limits S on small islands—habitat specificity, stochastic extinctions of small populations, or chronic disturbances. This temporal aspect of the passive sampling hypothesis has not been addressed in the literature and deserves further attention.

RECOMMENDATIONS

We recommend the passive sampling model as a simple null model for studying species-area relationships. If abundance data are available, Coleman’s (1981) analytic solutions can be used. If only presence-absence data are available, the Monte Carlo simulations of Simberloff and Gotelli (1984) can be used to estimate expected species richness. The passive sampling model can be refined by incorporating prevalence functions (Haila et al. 1983) and habitat availability (Buckley 1982) on islands. Temporal change in species richness can be tested with a Markov model (Simberloff 1983c), although estimation of transi-

tion probabilities may be problematic (Boecklen and Nosedal 1991; Clark and Rosenzweig 1994). Critical tests of the MacArthur and Wilson (1967) equilibrium model include evidence of population turnover (Simberloff 1976a), measurement of immigration and extinction rates as a function of species richness (Williamson 1981; Strong and Rey 1982), and documentation of a species-area relationship within equal-sized quadrats (Kelly et al. 1989). Further studies of the species-area slope or the best-fitting transformation will not allow for critical tests. Instead, researchers should concentrate on unique predictions associated with hypotheses for the species-area relationship (Table 8.1).