

SPECIES–AREA RELATIONSHIPS

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GLOSSARY

- relative abundance distribution** The frequency distribution depicting the number of species in a community as a function of the number of individuals comprising each species.
- species–area curve** A graphical depiction of the dependence of species richness on area.
- species–area model** A function used to describe species–area curves.
- species–area relationship** The dependence of the number of species in a sample region on the area or size of the region.
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A **SPECIES–AREA RELATIONSHIP** is simply the observation that the number of biological species found in

a region is a positive function of the area of the region. Species–area relationships are depicted graphically as a bivariate plot of species richness on the ordinate and area on the abscissa, a species–area curve (Fig. 1). Species–area relationships appear to be ubiquitous, having been observed for a wide array of taxa ranging from diatoms to fish, insects, birds, vascular plants, and mammals and for geographical entities such as islands, political entities, woodland, grassland, and cropland habitat patches, lakes, river drainages, and artificial substrates from microscope slides to synthetic sponges and slates.

I. INTRODUCTION AND UNDERLYING MECHANISMS

H. G. Watson first described the species–area relationship in 1835 by remarking that as the area of a county in England increases by a factor of 10 the number of plant species found in that county increases by a factor of 2. The long history of discourse on species–area relationships has evolved from a focus prior to the 1960s on its empirical utility in determining optimal sample size and sample number for community description, for determining the minimum area of a community, and in extrapolating predictions of species richness to areas larger than those sampled to a focus in the 1960s and 1970s on the mechanisms underlying the species–area relationship, in finding the best mathematical

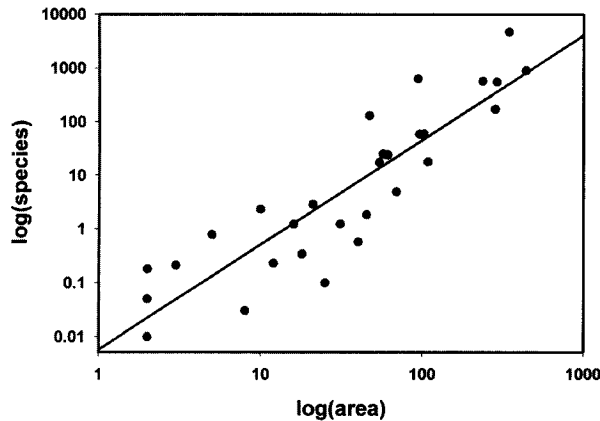


FIGURE 1 Species-area curve for the vascular plants of the Galapagos Archipelago. The logarithm of species richness is commonly plotted as a function of the logarithm of area, but species richness may also be plotted as a function of area or $\log(\text{area})$.

model for species-area relationships, and in explaining species-area relationships in the context of the equilibrium theory of island biogeography (Connor and McCoy, 1979). Since 1980, the primary focus of discussion involving species-area relationships has been their use and application in conservation biology to determine the optimal design of nature reserves and to project the expected loss of species richness from a region undergoing specified levels of area reduction (habitat loss). We review the discourse on species-area relationships beginning in the 1960s and focus our synthesis on the application of species-area relationships in conservation biology.

Three biological mechanisms have been proposed to account for species-area relationships: (1) the habitat diversity hypothesis, (2) the area per se hypothesis, and (3) the passive sampling hypothesis.

A. The Habitat Diversity Hypothesis

The habitat diversity hypothesis (Williams, 1964) proposes that the increase in species richness in large areas relative to small areas arises because large areas have a greater variety of habitats than small areas. This greater variety of habitats permits species that are only found in specific habitats to occur in large areas and permits species that require multiple habitats to persist in large areas, resulting in higher species richness in large areas than in small areas and the existence of species-area relationships. The habitat diversity hypothesis views

area as affecting species richness indirectly because of its association with habitat diversity rather than any direct effect of area on the ability of species to colonize or persist in larger areas. Studies that demonstrate positive correlations between the number of species and the number of habitats on an island have been viewed as supporting the operation of the habitat diversity hypothesis.

B. The Area Per Se Hypothesis

The area per se hypothesis (Simberloff, 1976) is based on the assumptions that the abundance of each species in a sample region varies as a positive function of that region's area and that the probability of each species going stochastically extinct in that area is a negative function of abundance, and therefore of area. Given these assumptions, large areas would have more species than small areas because more species would persist (not go locally extinct) in large areas. The area per se hypothesis suggests that even in a group of patches consisting of a single type of habitat, one would observe a species-area relationship. Correlations between species richness and area in studies that purport to examine a single habitat type and experimental studies that examine the consequences of reducing patch area are viewed as evidence supporting the operation of the area per se hypothesis.

C. The Passive Sampling Hypothesis

The passive sampling hypothesis (Connor and McCoy, 1979) conjectures that larger areas are more likely to receive more colonists than small areas and that these colonists are likely to represent a wider array of species than the pool of colonists arriving on small areas. Therefore, purely as a result of the higher abundance of colonists expected for large areas and independent of any increase in habitat diversity or reduction in extinction probabilities, one would expect more species to arrive on large areas, leading to species-area relationships. Several authors have examined the number of colonists arriving at their study sites and conclude that passive sampling accounts in part for the species richness of invertebrates on intertidal boulders, fish in stream pools and riffles, and birds on forest habitat islands. Each of these studies shows that for habitats that are colonized seasonally, those patches receiving more colonists have higher species richness.

Two other area-dependent factors that affect species richness have more recently entered discussions concerning species-area relationships, particularly for habitat patches: the resource concentration hypothesis and edge effects.

D. The Resource Concentration Hypothesis

The resource concentration hypothesis attempts to explain the phenomenon that habitat patches with large amounts of resources (e.g., monocultures, areas of high plant density, or large patches) have higher densities of insects. Therefore, the resource concentration hypothesis conjectures that population density should be positively correlated with patch area. In 1973, R. B. Root conjectured that the higher density of animals in larger patches might be solely a consequence of movement behavior (the movement hypothesis); herbivores are more likely to find, and remain in, large, monospecific stands of their host plant than in small or heterogeneous patches. If many species have higher population densities in large patches because of the resource concentration hypothesis, then extinction probabilities should be even lower than expected from the area per se hypothesis, and hence resource concentration could contribute to observed species-area relationships. E. F. Connor and co-workers have recently reviewed the existing literature on the relationships between animal population density and patch area and found for insects and birds that positive area-density relationships are common, but not so for mammals.

E. Edge Effects

Edge effects, or habitat edge dependent changes in abundance or risk of mortality, have been reported for species in a variety of taxa in habitat patches. Given that the proportion of a patch that occurs within any fixed distance from its edge is inversely related to area, edge effects could lead to species-area relationships even within a single habitat type. Such an edge effect on species richness would be mediated by a reduction in the abundance of a species on small patches because of a larger amount of "edge habitat," leading to higher probabilities of local extinction. Therefore, part of the dependence of species richness on area that has pre-

viously been attributed to area per se may actually be caused by edge effects.

F. Multiple Causes of Species-Area Relationships

Habitat diversity, area per se, passive sampling, edge effects, and resource concentration are not mutually exclusive mechanisms and may operate individually or in combination to cause species-area relationships (Connor and McCoy, 1979). Experiments on invertebrate colonization on artificial substrates of varying size and habitat diversity clearly demonstrate the joint contribution of habitat diversity and either the area per se or passive sampling hypothesis, or both, to the generation of species-area relationships. Studies that subsampled islands using a constant-sized quadrat on each island in an attempt to eliminate the effect of habitat diversity found strong effects of habitat diversity, but species richness remained a positive function of island area even for data derived from constant-sized quadrats. Using path analysis, D. D. Kohn and D. M. Walsh concluded that area had both a direct effect on species richness (area per se and/or passive sampling) and an indirect effect mediated by the effect of area on habitat diversity.

The evidence that would allow one to clearly partition the causes of a specific species-area relationship among these underlying mechanisms is exacting. Habitat diversity is difficult to measure, and edge effects might make it impossible to separate the effects of increasing area from the effects of area on habitat diversity. The area per se, resource concentration, and passive sampling hypotheses act by affecting the abundances of species on an island. Area per se and resource concentration do so by reducing extinction probabilities via allowing larger populations (or more dense populations) to persist on large islands, and passive sampling does so by proposing that greater numbers of colonists arrive on large islands. To demonstrate an effect of area per se or resource concentration, one must ultimately show that species on average have larger population sizes (or in the case of resource concentration, higher population densities) and lower extinction probabilities on large islands or habitat patches. To demonstrate an effect of passive sampling, one must show that the arrival rate of colonists on large islands or habitat patches is greater than for small patches and that the colonizing individuals arriving on large patches comprise a greater number of species than those arriving on small patches.

To demonstrate that edge effects contribute to species-area relationships would require evidence that species absences from small patches could be uniquely attributed to edge effects and not to the alternative mechanisms discussed above.

II. SAMPLING AND STATISTICAL PRACTICE IN DESCRIPTION OF SPECIES-AREA RELATIONSHIPS

A. Sampling Practice

Two main sampling schemes have been used to generate data on the relationship between species richness and area. The most widely used approach has been to sample physically separated areas such as islands or habitat patches or to sample adjacent or abutting areas of continuous habitat as independent, nonoverlapping replicates (Fig. 2). For physically separated areas, sampling from the observed natural range of areas generates a range of sample areas. For continuous habitat, the re-

gion is divided arbitrarily into a series of nonoverlapping subregions to generate a range of sample areas. The alternative approach, which has been used widely by plant ecologists, is to enumerate the locations of species within a larger region and generate a sample of areas by subsampling a range of areas within the larger region. These subsamples may be overlapping or not, depending on the choice of the researcher (Fig. 2).

1. Independent Areas

Physically independent sample areas have been widely used because species-area data could be readily generated for natural geographical units, such as islands, by combining published monographic species lists with published data on island areas. The majority of species-area curves were published in the 1960s and 1970s by scientists gleaning existing data on the monographic literature and combining data on species richness with published estimates of area. Species-area curves based on gleaned data could be produced relatively quickly via a trip to the library. Another advantage of using physically independent sample areas is that they are

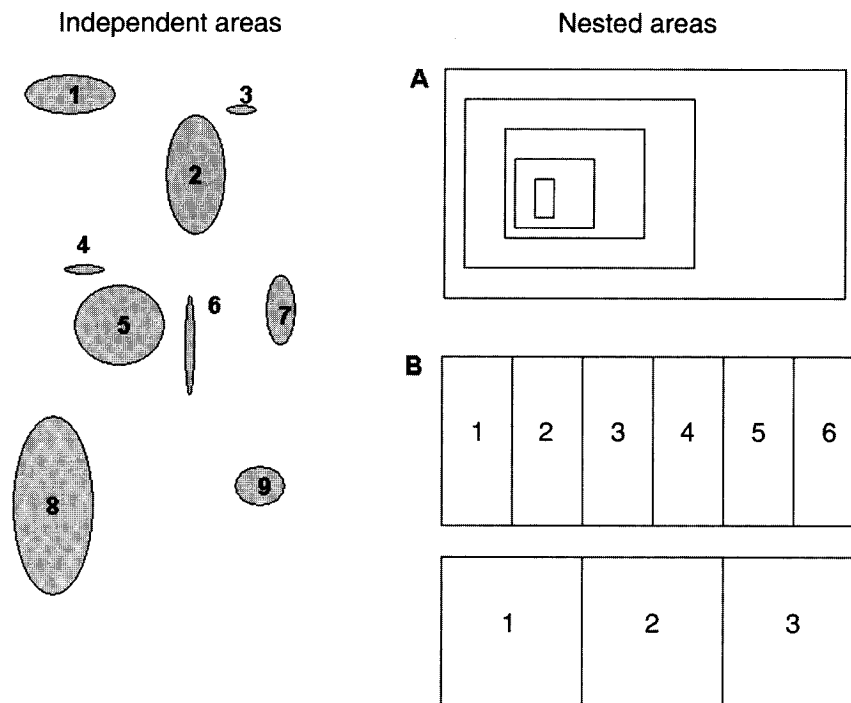


FIGURE 2 Independent and nested sampling designs used in species-area studies. Independent areas are physically separate. Nested areas may be serially self-contained as in A or abutting as in B. If abutting areas are used, then the sampled region is partitioned into a series of equal-sized, adjacent areas, and this process is repeated for the range of different sized areas. Only two areas are depicted in B, one with six replicates and one with three.

arguably also statistically independent. The statistical independence of separate, nonoverlapping areas allows use of the methods of statistical inference and hypothesis testing associated with ordinary least-squares (OLS) regression. The application of OLS regression permitted the estimation of the parameters (and their standard errors) for any of the proposed functional forms of the species-area relationship that could be made sufficiently linear by transformation of the data and an assessment of the statistical significance of the fit of a particular model. Furthermore, the use of statistically independent areas allowed the rigorous comparison of parameter estimates between studies via analysis of covariance or other simpler techniques.

2. Nested Areas

Plant ecologists have generated data for many years on the relationship between species richness and plot or quadrat area for a variety of plant communities. Much of this work was done to determine the optimal plot size to use when describing plant communities. Presumably because of the saving in sampling effort, plant ecologists used serially self-contained or nested quadrats rather than physically independent quadrats to determine optimal quadrat size. However, nested quadrats are not statistically independent so it is inappropriate to use OLS regression to fit a linear model to such data and assess the fit of the model or estimate its parameters. Therefore, use of nested quadrats to examine species-area relationships in plant communities was largely discontinued by the end of the 1970s. Recent research programs aimed at understanding the structure and dynamics of tropical forests have once again led to studies of species-area relationships using nonindependent data. However, Condit *et al.* (1996) partition their largest quadrat into as many equal-sized quadrats as possible and use the mean for all nonoverlapping quadrats to estimate species richness for that quadrat size. They repeat this process of partitioning their large quadrat (50 ha) into the maximum number possible of nonoverlapping subquadrats for a variety of quadrat sizes. Condit *et al.* (1996) then plot the mean and standard error of species richness for each quadrat size as a function of quadrat area to produce a species-area curve. This approach leads to appropriate estimates of species richness and its standard error for each individual quadrat size, since within a size category the quadrats used to estimate the mean and standard error of species richness are independent. However, since the same sampled area is used to estimate species richness for each quadrat size, these estimates are not statistically independent and Condit *et al.* (1996) appropriately re-

frain from using regression techniques that require independence to fit statistical models to species-area data.

B. Statistical Practice

OLS regression has been used to fit models to species-area data. By applying OLS regression, estimates of the model's parameters and their associated standard errors can be obtained readily. If one makes the additional assumptions that the model's errors are independent, homoscedastic, and normally distributed and that species richness or the logarithm of species richness is a linear function of area or its logarithm, then rigorous statistical inferences about the parameters may be made. In recent years, nonlinear regression procedures have become widely available so that inherently curvilinear species-area models may be directly fit to data. Nevertheless, OLS regression continues to be used widely.

P. J. Vincent, J. M. Haworth, and M. R. Williams point out that the assumptions of normality and homogeneity of error variances are unlikely to be met by species-area data. First, species richness is unlikely to be normally or log-normally distributed and probably should be treated as a discrete, rather than a continuous, variable. Second, the variance in species richness is likely to be a function of the mean species richness. These properties arise in part because on very small areas both the mean and variance of species richness must be nearly zero. Vincent and Haworth suggest analyzing species-area data using a generalized linear model and treating species richness as a Poisson-distributed variable. Williams also suggests analyzing species-area data using a generalized linear model but recommends that species richness be treated as a binomially distributed variable (see discussion of Williams' extreme value model below). In both cases, parameters and their standard errors can be estimated and rigorous statistical inferences can be made. Unfortunately, few authors have explored the treatment of species-richness data as Poisson or binomial variables in studies of species-area relationships.

III. FUNCTIONAL FORM OF THE SPECIES-AREA RELATIONSHIP

When species richness is plotted as a function of area, the resulting plot is a curve that may be linear, concave downward, concave upward, or sigmoid (Fig. 3). The shape of species-area curves appears to be a function of the particular range of areas studied, and this may,

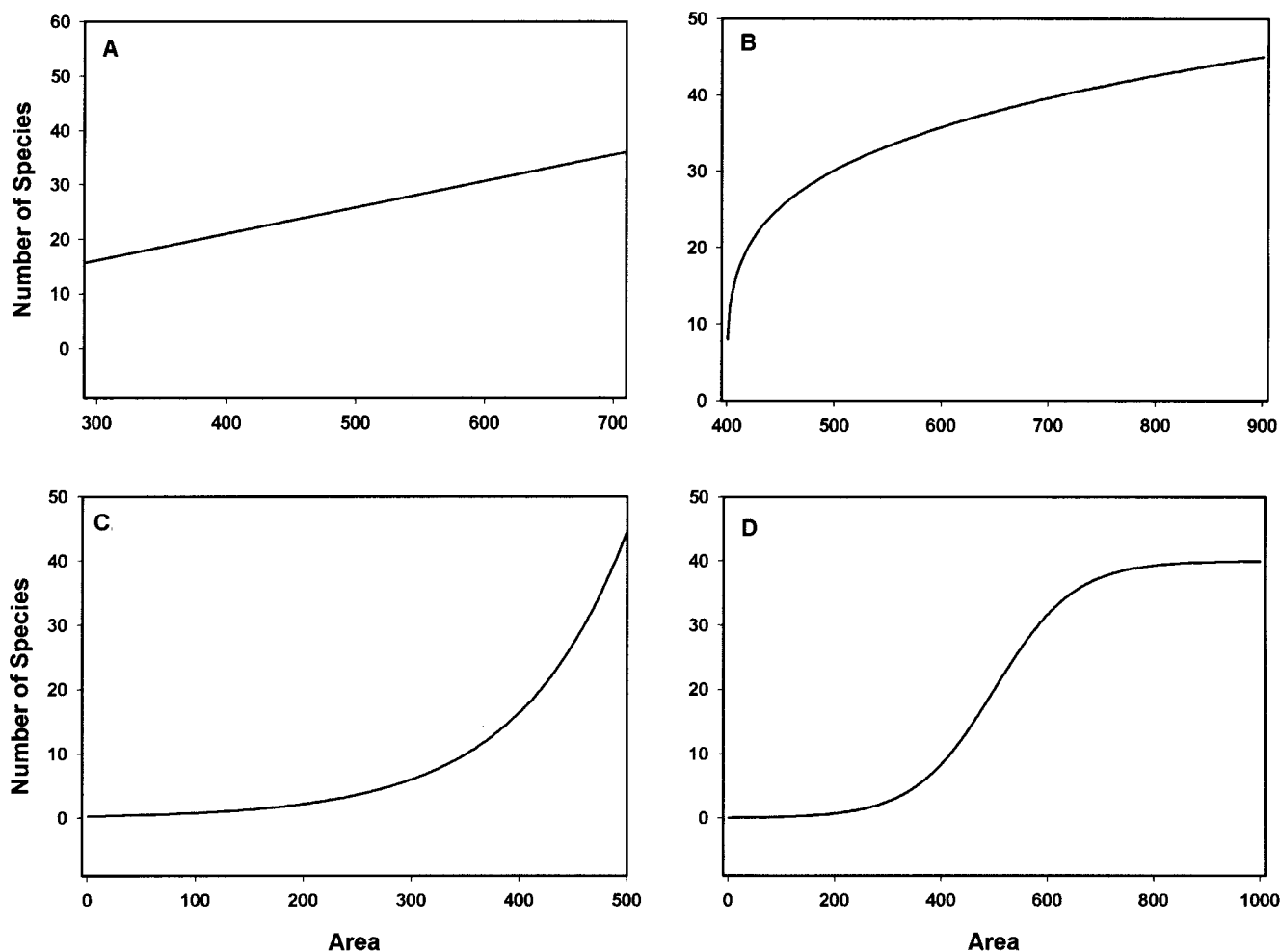


FIGURE 3 Shapes of species–area curves encountered in empirical studies: (A) linear species–area curve; (B) concave-downward species–area curve (linearized by the log–log transformation); (C) concave-upward species–area curve (linearized by a semilogarithmic transformation, area log-transformed); (D) sigmoid species–area curve (usually not transformed). Linear curves are encountered at intermediate spatial scales, concave-downward curves at larger spatial scales, concave-upward curves at small spatial scales, and sigmoid curves when a wide range of spatial scales is studied.

in part, explain the variety of transformations used to linearize species–area curves.

Historically, much of the discussion of species–area relationships focused on the specific functional form of the relationship between species richness and area. In 1921, O. Arrhenius proposed that species–area relationships followed a power function (Fig. 3B):

$$S = cA^z,$$

which, for statistical convenience, has commonly been approximated by the log–log transformation:

$$\log S = \log c + z \log A,$$

with c and z as constants. The double-logarithmic transformation linearizes the power-function model, so that species–area curves are linear on a double-log plot (Fig. 1). In 1922, H. A. Gleason championed an exponential model of the species–area relationship (Fig. 3C):

$$S = \log c + z \log A,$$

because he observed the power-function model to predict impossibly large numbers of species for large areas. The exponential model produces species–area curves that are linear on a semilogarithmic plot. Both of these models were supported because they seemed to fit specific data sets using independent areas reasonably well

and because it was argued that they could be derived as a consequence of assuming that the distribution of individuals among species (the relative abundance distribution) was either log-normal or log-series, respectively. Other ecologists reported that when a wide range of areas were sampled, neither the power-function model nor the exponential model fit their data since species-area curves appeared sigmoid in shape (Fig. 3D).

Connor and McCoy (1979) examined the fit of the power-function model, the exponential model, and two other models to data from 100 species-area studies. They found that while the power-function model often fit the data well, it was not found to be the best fit model substantially more often than other models. Based on this analysis, the observation that the log-log transformation can linearize a wide range of curves, and because of its widespread use, Connor and McCoy (1979) recommended continued use of the power-function model of species-area relationships.

Recent discussions of the functional form of the species-area relationship have continued to promote use of the power-function model but have continued to justify its use because of its hypothesized connection to log-normal relative abundance distributions (Rosenzweig, 1995). Given a common log-normal relative abundance distribution from which the abundances of species on all sites (islands or habitat patches) arise, it is possible to derive species-area data that are reasonably well fit by a power-function model. However, simply because a particular set of species-area data is reasonably well fit by a power-function model does not imply that this fit derives as a consequence of sampling from a common log-normal relative abundance distribution (Hanski and Gyllenberg, 1997). Many island archipelagos are colonized from multiple source regions rather than from a single source pool, and individual islands within such archipelagos may receive differing proportions of their colonists from each source. On the other hand, habitat patches may be more accurately viewed as units whose species composition is determined by sampling from a source pool with a single relative abundance distribution.

Continued debate about the functional form of the species-area relationship assumes that underlying the variability we observe in empirically estimated species-area curves lies a single true function that will characterize this relationship. However, most data on species-area relationships using independent areas have small sample sizes, cover a narrow range of areas, and may be confounded by area-dependent sampling effort, among other problems. Given the quality of the data available, it will be devilishly difficult to discern the functional

form of the species-area relationship, even if a single form exists. Furthermore, it is possible that differences among taxa or spatial scales could generate species-area relationships of different functional forms.

A. Self-Similarity and the Power-Function Model of Species-Area Relationships

J. Harte and co-workers have recently proposed an alternative derivation of the power-function model of the species-area relationship. This derivation comes from examining nested areas and making the assumption that successive partitions of a continuous area have the fractal property of "self-similarity." That is, the distribution of species in successive partitions is independent of spatial scale. Beginning with a large continuous area A_0 with S_0 species, bisections of A_0 such that the rectangles comprising the two halves of A_0 have area $A_i = A_0/2^i$ each will have on average S_i species, where i indicates the i th bisection of A_0 . The assumption of self-similarity requires that a species known to be in A_i will have probability a of being found in at least a specific one of the two rectangles of area A_{i+1} created by bisection, and therefore that the fraction of species found in A_i that are found in a specific one of the A_{i+1} rectangles equals the same constant a for all i bisections. The constancy of a for all i bisections follows from the assumption of self-similarity since a , the probability of occurrence in a half-patch under bisection, must be independent of spatial scale. Harte *et al.* (1999) show that the assumption of self-similarity leads directly to the power-function model of the species-area relationship: $S_i = cA_i^z$, with the self-similarity parameter $a = 2^{-z}$. Furthermore, since under successive bisections of an initial continuous area the value of a must lie between 0.5 and 1, the relationship between a and z dictates that the slope of the power-function model, z , must lie between 0 and 1. Hence, the power-function model of the species-area relationship is derivable without recourse to any assumptions about the underlying relative abundance distribution of species.

Harte and colleagues have extended the assumption of self-similarity to generate an expectation for the relationship between the number of endemic species and area and the expected spatial turnover between two patches isolated by a known distance, d . These extensions of the assumption of self-similarity provide a basis for estimating the expected loss of species from areas undergoing habitat reduction, for calculating z from spatially separated sites, and for estimating species richness at spatial scales larger than commonly possible in previous studies of species-area relationships. However, as Harte and colleagues point out, the assumption

of self-similarity is not likely to hold for a wide range of spatial scales, so care must be taken to test the assumption of self-similarity for the taxa and spatial scales of inference. While Harte and colleagues have published a few examples where the assumption of self-similarity seems reasonable over a specific range of spatial scales, Plotkin and colleagues show that tropical forest trees are not self-similar in distribution over spatial scales from 1 to 10^3 m².

B. Extreme Value Model and Random Placement

An alternative model of species-area relationships based on "random placement" was first proposed by B. D. Coleman in 1981 (Coleman *et al.*, 1982) and extended by Williams (1995). The random placement model of species-area relationships derives the expected number of species on a site, $\bar{s}(\alpha_k)$, of area A_k as a consequence of placing the n_i individuals of the i th species on sites independently and at random with probability $\alpha_k = A_k/A_i$, where A_k is the area of the k th site, A_i is the combined area of all sites, and S is the total number of species among all sites:

$$\bar{s}(\alpha_k) = S - \sum_{i=1}^S (1 - \alpha_k)^{n_i}$$

As presented by Coleman *et al.* (1982), data on the total abundance of each species combined among all sites were required to estimate the expected species-area curve under the random placement model. Because the random placement model required data that ecologists seldom have, censuses of the abundances of each species at each site, and because this model does not yield fitted parameters comparable to other species-area models, few authors attempted to fit the random placement model to their data.

Williams (1995) extended and adapted the random placement model to be approximated by an extreme value function which permits model fitting within the context of the generalized linear model and requires data only on species richness and area, not the abundances on the individual species. The extreme value function model of species richness, \bar{s} , in $\log A$ is then

$$\bar{s} = P[1 - \exp(-\exp(y \log A + \log d))],$$

with P being the number of species in the species pool, and y and $\log d$ the slope and intercept of the model, respectively. Williams (1995) outlines a method for

estimating P if the species composition of the biota is unknown but suggests that the best estimate of P is the total number of species found. The extreme value function model has been fit to a limited number of data sets but appears sigmoid when species richness is plotted as a function of $\log(\text{area})$. The random placement/extreme value function model of species-area relationships is appealing because it is derived under a hypothesis of independence within and between species. However, as Williams (1995) points out, discriminating between the power function and the extreme value function models with most existing data sets derived from sampling independent areas will be difficult.

IV. INTERPRETATION OF THE PARAMETERS OF SPECIES-AREA MODELS

The widespread use of the power-function model of the species-area relationship coupled with specific numerical expectations for its slope parameter, proposed by F. W. Preston in 1960, led to numerous attempts to infer biological significance to values of this parameter. The slope parameter measures the rate at which species are added as area increases, and the intercept parameter has been considered a function of taxon-specific attributes and environmental variation. Only a limited attempt has been made to offer biological interpretations of the intercept parameter, partly because in the power-function model the absolute value of c depends on the units in which area is measured (Connor and McCoy, 1979; Rosenzweig, 1995). The parameters of other models of the species-area relationship have generally been treated as fitted statistical constants, with no attempt to interpret them biologically.

The slope of the power-function model of the species-area relationship and patterns of variation in this parameter have been subjected to considerable analysis and interpretation. Connor and McCoy critiqued many of these interpretations in their 1979 review. We briefly examine a few of these interpretations and touch on those proposed more recently.

A. Canonical Slope Values

F. W. Preston proposed that isolated islands in equilibrium that sample colonists from a common log-normal relative abundance distribution with parameter $\gamma = 1$ (Preston's canonical hypothesis) will have a slope of

0.262 in the power-function model. He subsequently broadened the range of slope values that he expected from isolates to values between 0.17 and 0.33. R. M. May showed in 1975 that using a wide range of log-normal parameter values leads to power-function slope values in the 0.15–0.39 range. Many authors have generated slopes from the power-function model of the species–area relationship and interpreted values in the range of 0.2–0.4 to be consistent with Preston's idea that species–area curves arise because the species richness of islands results from sampling from an underlying log-normal relative abundance distribution. However, Connor and McCoy (1979) challenged Preston's idea of a canonical range of slope values by showing that slopes in the 0.2–0.4 range are expected purely as a consequence of the tendency to publish studies that show a high correlation between species richness and area and because the variance in species richness will always be less than the variance in area. Connor and McCoy (1979) concluded that slope values from the power-function model of species–area relationship in the 0.2–0.4 range could not be used as evidence for the existence of an underlying log-normal relative abundance distribution.

B. Island–Mainland Differences in Slope Values

Preston extended his idea that islands or isolates should have power-function slopes in the 0.2–0.4 range to project that nonisolated or mainland areas should have lower slope values than isolated areas. His rationale derived from his belief that nonisolated areas would sample from a truncated relative abundance distribution with a higher ratio of species to individuals. In their monograph "The Theory of Island Biogeography," MacArthur and Wilson (1967) modified Preston's idea, suggesting a specific range to be expected for slopes derived from nonisolated areas, 0.12–0.19, and explaining the lower slopes as arising because of the "transient hypothesis." The transient hypothesis suggests that more transient individuals will be encountered in small, nonisolated areas than in small, isolated areas, which, in turn, will lead to more species being encountered on small, nonisolated areas than on small, isolated areas. The greater number of species found on small, nonisolated areas would depress the slope of the species–area curve for mainland areas relative to that expected for islands. The available evidence, while limited, is consistent with the idea that power-function slopes for mainland areas are lower than those for islands.

Hanski and Gyllenberg (1997) develop dynamical models of species incidence that generate predictions about the slopes of species–area curves as a function of the moments of the relative abundance distribution and the ratio of species' colonization and extinction rates. Hanski and Gyllenberg (1997) develop two models, one in which sites are colonized from an external source, their "island–mainland model," and one in which the sources of colonists are internal to the system of sites, their "metapopulation model." They find that species–area slopes are lower for their metapopulation model and claim that such a model is analogous to mainland areas, while their island–mainland model is analogous to truly insular situations. Hanski and Gyllenberg (1997) suggest that their models imply that the observation of lower slope values on mainland sites is a result of metapopulation dynamics rather than the transient hypothesis.

C. The Effect of Isolation on Slope Values

MacArthur and Wilson extended their transient hypothesis to predict that the slopes of species–area curves should be lower for distant archipelagos of islands than for islands located close to mainland areas. However, T. W. Schoener illustrated with species–area curves for birds in 23 archipelagos that exactly the opposite pattern occurs. Schoener's result suggests that the slope of species–area curves depends on the size of the source pool of colonizing species, which would be smaller for distant than near island groups. In other words, the low slopes for species–area curves observed for isolated archipelagos tell us no more than that isolated biotas are depauperate. Hanski and Gyllenberg (1997) suggest that Schoener's observation of lower slope values for isolated archipelagos arises because isolated archipelagos behave according to their metapopulation model, not as an island–mainland system.

D. Other Interpretations of Slope Values

Many other efforts have been made to explain variation in the slope of the power-function model of the species–area relationship. These efforts include (1) attempts to equate the slope of the species–area curve with β , or between-habitat diversity, and the intercept with α , or within-habitat diversity, (2) attempts to predict patterns in the latitudinal dependence of the species–area relationship (both slope and intercept), and (3) attempts to identify taxonomic and trophic group differences in species–area curves, among others. Connor and McCoy (1979) critiqued many of the attempts to interpret the

parameters of the power-function model of the species-area relationship and recommended that these parameters be viewed as fitted constants, with no specific biological interpretation.

E. Conclusions

Species-area relationships represent a pattern expected in nature that may arise from the colonization and development of quasi-independent biotas on islands or habitat patches (island-colonization model) or from the loss, reduction, and fragmentation of a previously continuous or widespread biota into remnant habitat patches (mainland-vicariance model). Historically, inquiry into the mechanisms underlying the species-area relationship and its functional form has been biased toward the island-colonization model. However, models based on self-similarity more closely represent the mainland-vicariance model and provide a basis to unify species-area relationships with other patterns in the geographical distribution of species (e.g., distribution and abundance relationships, compositional similarity among sites, and relative abundance distributions). Continued empirical study of the species-area relationships and inquiry into the functional forms expected under specific biological and sampling models will continue to improve our understanding of spatial patterns of species richness.

V. USE OF SPECIES-AREA CURVES IN CONSERVATION BIOLOGY

What can an understanding of the species-area relationship contribute to the preservation of biodiversity? The question has interested ecologists for more than 30 years since the pioneering work of N. W. Moore, E. Maarel, and others and has led, almost from the beginning, to a bewildering confusion of missteps and dead ends (see Shafer (1990) for an overview). Implicit in this question are the important assumptions that species richness is the primary object of preservation and that area is the primary influence on species richness. Here, we shall explore two separate, but similar, aspects of the question. We shall see what ecologists have been able to conclude about the loss of species accompanying area reduction and what they have been able to conclude about the best way to slow the loss.

A. Loss of Species from Area Reduction

As we have illustrated, the species-area relationship is an extraordinarily common pattern in nature, and it

has been documented numerous times. It would seem, therefore, that calculating the loss of species accompanying a certain amount of area reduction would be a rather straightforward exercise. All that one would need to know to perform the calculation would be the original number of species (S_{original}), the amount of area reduction ($A_{\text{reduced}}/A_{\text{original}}$), and the slope of the species-area relationship (z). For example, if one assumes a power-function model of the species-area relationship ($S = cA^z$), then $S_{\text{original}} = c(A_{\text{original}})^z$, $S_{\text{reduced}} = c(A_{\text{reduced}})^z$, and, therefore, $S_{\text{reduced}}/S_{\text{original}} = (A_{\text{reduced}}/A_{\text{original}})^z$ (Fig. 4). Although calculations of this sort are reasonably com-

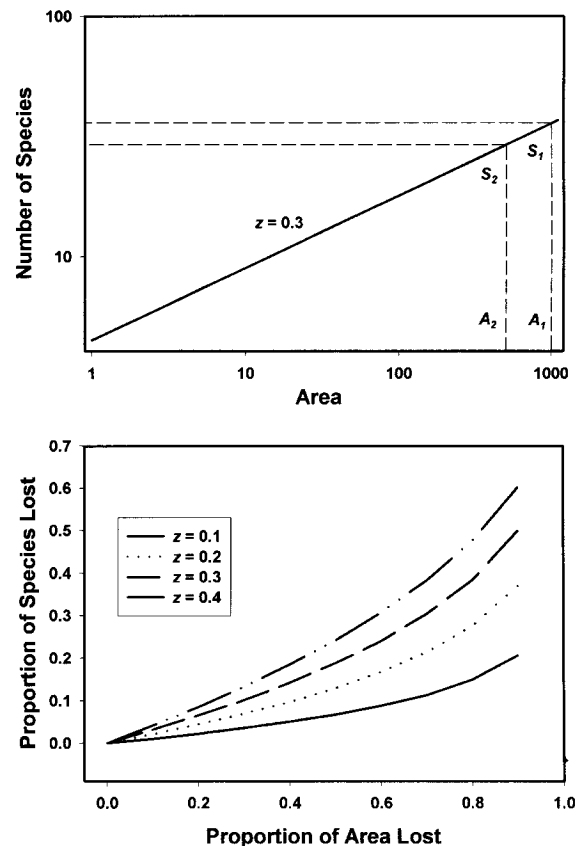


FIGURE 4 Loss of species richness under specified levels of habitat loss expected using the power-function model of the species-area curve. (A) Illustrates the SLOSS controversy calculation of the number of species expected for a single large reserve of 1000 units of area (34.5 species) versus the number of species expected for a reserve half that size (500 area units), 29 species. If the species lists from the two half-sized reserves do not overlap extensively, then the two half reserves should contain more species than the single large reserve. For this example, $S = 4.5A^{0.3}$. (B) The expected proportion of species lost when area is reduced by a fixed proportion as calculated using the power-function model of the species-area relationship for various values of z and $S = 4.5A^z$.

mon, they require at least five assumptions. First, area reduction completely eliminates species that were originally present (but some species may survive on relict fragments or disturbed lands). Second, all of the species that were originally present were distributed homogeneously (but most species are unlikely to be distributed in this manner). Third, an appropriate model has been selected to describe the species-area relationship. Fourth, the slope of the species-area relationship is accurate and a constant (but it is not likely to be, for a number of reasons). Fifth, the loss of species is a direct consequence only of area reduction (but it is not likely to be, for a number of reasons). The last two assumptions have received the most attention from ecologists. We shall discuss both of them further.

Correct choice of the slope of the species-area relationship is critical. Clearly, if one knew the original number of species and area and the reduced number of species and area, then the slope would be determined precisely. The point of the calculations presented above, however, is to estimate potential species loss, before it happens, so the slope of the species-area relationship also must be estimated, from theory and empirical study. A great deal of uncertainty accompanies such estimation. First, one must decide which model of species loss is appropriate. For example, if the relationship between species and area were assumed to be linear (Fig. 3A), then a much different rate of loss of species would be predicted to occur than if the relationship were assumed to be a power function (Fig. 3B). Second, one must assume that the slope of the species-area curve is constant between the spatial scales over which species loss is to be estimated. A nonconstant slope value would suggest that an appropriate species-area model has not been completely specified and could lead to substantial misestimation of species loss. Third, one must decide if the reduced area better represents an isolate (a "true" island) or simply a subsample of the original area. Typically, slopes of species-area relationships are greater in the first case (approximately 0.20–0.40, on a log-log scale) than in the second (approximately 0.12–0.19, on a log-log scale). Furthermore, it may be that the reduced area could come to function less like a subsample and more like a true island over time, so that the range of potential slopes could expand dramatically over time. Fourth, even if one managed to choose the more accurate of the two ranges of slope values, an impressive amount of variation would still remain. For example, with the equations presented above, if area is reduced by 80% and $z = 0.20$, then species loss is estimated at 27%, whereas if area is reduced by the same percentage but $z = 0.30$, then species

loss is estimated at 38%. Fifth, even if one knew precisely the correct slope of the species-area relationship in one location at one time, Connor and McCoy (1979) and others have shown that slope is not likely to be amenable to translation across locations, latitudes, or time.

One empirical means for focusing the choice of slope values is the body of literature documenting decline in species richness accompanying area reduction. J. M. Diamond termed this process "relaxation." A number of studies, for example, have examined the relaxation in the species of mammals that may have occurred on nature reserves, both in North America and in Africa. The results of these studies clearly illustrate the difficulty in choosing a slope of the species-area relationship. For African savanna reserves, R. East has shown that estimates of species loss accompanying a 100-fold reduction in area vary from about 40% to more than 90%, depending on the required minimum viable population size (i.e., the population size that ensures persistence with a certain probability for a certain length of time). W. D. Newmark has shown that similar high variability exists for western North American national parks.

At least three potential reasons underlie the poor predictability generally seen in studies of relaxation. The first two reasons, the presence of statistical or sampling errors and the lack of sufficient time since area reduction took place to allow full relaxation, could be addressed by careful experimentation. The protocol is to document the species richness of a relatively large area, reduce the area, and then document the species richness of the reduced area. Unfortunately, most of these kinds of experiments have been carried out at such a small scale that their general value at the scale of typical nature conservation efforts is questionable. Slope values derived from these experiments are, therefore, not likely to be of much practical value. A few reasonably large scale experiments in area reduction have been undertaken, most notably The Minimum Critical Size of Ecosystem project of D. H. Janzen, T. E. Lovejoy, R. O. Bierregaard, and others. These relatively large scale experiments suggest that the species-area relationship alone does not predict species loss particularly well. Slope values derived from these experiments, therefore, also are not likely to be of much practical value. The third reason, lack of the autecological (i.e., species-specific ecological) information needed to infer that the loss of species is attributable directly to relaxation, cannot be addressed as readily by experimentation.

Recall that one of the assumptions necessary to pre-

dict loss of species accompanying area reduction was that the loss of species is a direct consequence only of area reduction. Loss of species actually may occur only as an indirect consequence of area, because of some factor that happens to be correlated with area reduction, such as level of disturbance, complexity of habitat structure, or—probably most importantly—fragmentation. It seems clear that in virtually all real-world cases, area reduction is likely to be accompanied by fragmentation. That is, one relatively large area is not likely to be reduced to a single relatively small area, but rather to an archipelago of relatively small fragments. For example, Simberloff (1992) has shown that fragmentation effects, as well as size-dependent habitat changes, are at least as important as area reduction in predicting species loss in the relatively large scale experiments mentioned previously. It has been known for quite some time, at least since the pioneering work of N. W. Moore and others, that fragmentation can have adverse effects on organisms, independently of the effects of area reduction. The species–area relationship predicts that each of the fragments will support fewer species than the original area, but it alone cannot predict the cumulative number of species in the entire archipelago of fragments. As D. Simberloff and L. G. Abele have clearly shown, we also must know the degree of overlap in the species compositions of the fragments. If, for example, the compositions of the fragments were identical, then the archipelago would support fewer species than the original area. If, on the other hand, the species compositions of the fragments did not overlap at all, then the archipelago could support as many—or, potentially, even more—species than the original area. Assuming, realistically, that compositions overlap to an intermediate degree, calculating the loss of species by the method we have just illustrated could yield either an underestimate, if many species were confined to but a small subset of fragments, or an overestimate, if they were not. Fragmentation, therefore, adds more uncertainty—the degree of overlap in species compositions—to any prediction of the loss of species accompanying area reduction. We could predict the degree of overlap in the species compositions of fragments better if we had detailed information on the habitat requirements and minimum viable population sizes of individual species and on spatial variation in species richness, but as Simberloff and others have shown, such information is notoriously difficult to obtain and, therefore, is in very short supply.

Recently, a method has been suggested by Harte and co-workers whereby the slope value for species–area relationships among fragments might be obtained more easily. This method is based on the idea of self-similarity that we discussed previously. Essentially, the method

requires only measurement of the degree to which species lists in separated, small, censused patches overlap as a function of the distance between patches and the area of the patches. Self-similarity, then, allows translation of the resulting slope value across scales, so that censusing of prohibitively large areas or obtaining extensive autecological information becomes, in theory, unnecessary. A. P. Kinzig and J. Harte have also developed a procedure for estimating species loss from habitat reduction that derives from the assumption of self-similarity and from examining the relationship between the number of “endemic species” and area, an endemics–area relationship (EAR). In the examples examined thus far, the estimated species loss from area reduction is less using Kinzig and Harte’s EAR approach than from the traditional approach based on the species–area relationship outlined above. Whether these approaches to estimating species–area slopes and calculating species loss will lead to yet another dead end remains to be determined but will depend on how reasonable it is to assume self-similarity over a range of spatial scales.

B. Slowing the Loss of Species

In the previous section, we explored what the species–area relationship was able to tell us about species loss accompanying area reduction. In this section, we shall explore what the relationship can tell us about slowing that loss. In doing so, we shall treat area reduction with concomitant loss of species as an accomplished fact and concern ourselves solely with maximizing the remaining species richness. We shall, in turn, focus on maximizing species richness by the judicious choice, or design, of nature reserves.

The serious study of the relationship between the species–area relationship and the design of nature reserves began in the mid-1970s. At that time, several papers by J. Terborgh, J. M. Diamond, E. O. Wilson, E. Willis, and others came out more or less simultaneously touting the overarching importance of largeness of nature reserves. Some of these papers maintained further that the species–area relationship indicates that nature reserves should be subdivided as little as possible, that is, that a single intact reserve of a certain area will support more species than a series of individually smaller reserves that are cumulatively of the same area. Diamond, for example, said “many species that would have a good chance of surviving in a single large reserve would have their survival chances reduced if the same area were apportioned among several smaller reserves.” The basic problem with these ostensibly reasonable proposals—call them largeness and singularity—is that they may be too simplistic for real-world conservation

challenges. They may be too simplistic because of the substantial set of assumptions that accompanies them. We shall address perhaps the most basic of these assumptions in detail. This assumption is that the importance of largeness and singularity follows directly from the species-area relationship.

Most of the early papers based their arguments for largeness and singularity on R. H. MacArthur and E. O. Wilson's theory of island biogeography. This theory of island biogeography takes a dynamic view of the maintenance of species richness on "islands," as a balance between colonization and extinction. The resulting species richness, therefore, is considered an "equilibrium number of species." If relatively large areas support relatively large populations, then relatively large areas also should have relatively low extinction rates and, consequently, support relatively high equilibrium numbers of species. Accordingly, any subdivision of a relatively large area essentially creates smaller areas, each with higher extinction rates, so that the equilibrium number of species on each of the areas necessarily will fall ("relaxation"). The early papers also made a variety of proposals to enhance colonization, reflecting the potential importance of clustering and corridors and of shape, but we shall not address these proposals.

Almost immediately, the arguments for the overarching importance of largeness and singularity were challenged. Simberloff and Abele showed that the species-area relationship did not unambiguously favor a single intact reserve over an archipelago of smaller reserves. For example, if one assumes a power-function model of the species-area relationship ($S = cA^z$) and that $A_{\text{small}} = A_{\text{large}}/2$, then the number of species in the large reserve is $S_{\text{large}} = c(A_{\text{large}})^z = c(2A_{\text{small}})^z = 1.2S_{\text{small}}$ (Fig. 4). This equation could yield $S_{\text{large}} < 2S_{\text{small}}$ in a variety of realistic circumstances. Subsequently, R. W. Rafe elaborated the mathematical underpinnings of the comparison of the relative abilities of a single large reserve (SLR) and two reserves of half the area (THR) to support species. R. W. Rafe, A. J. Higgs, M. B. Usher, and others clearly illustrated that the proportional overlap of species between the smaller reserves is a critical issue. In essence, the greater the overlap, the more a single large reserve is favored, and vice versa. The relevant, and critical, information necessary to predict the amount of overlap mostly is lacking, a fact mentioned early on by Simberloff and Abele in response to criticisms of their analysis.

By the early 1980s, the controversy over choice of nature reserves had evolved into the "single-large-or-several-small (SLOSS) debate." O. Järvinen, D. Simberloff, L. G. Abele, and others emphasized, once again, that the species-area relationship—or the underlying island biogeographic theory, for that matter—did not

unambiguously favor a single intact reserve over an archipelago of smaller reserves. That some species might need relatively large areas for their continued well-being, while others could thrive in, or actually required, certain relatively small areas, had become well established in the ecological literature, beginning with the early work of J. Terborgh, R. T. T. Foreman, and others, so their proposal should not have been very controversial. Such was not the case, however, and the debate continued. In 1986, M. E. Soulé and D. Simberloff gave the SLOSS debate last rites: "The SLOSS debate is no longer an issue in the discussion about the optimal size of nature reserves." Yet, rumors of the death of the SLOSS debate were greatly exaggerated, for it continued beyond the middle of the 1980s—briefly mutating into the SLOPP ("single-large-or-plentifully-patchy") debate of M. E. Gilpin in the late 1980s—right up to today.

M. E. Soulé and D. Simberloff suggested that the truly important remaining question was "the dynamics of species extinction after the reserves are set up and surrounded by habitat modified by human activities," as had J. A. Kushlan, H. Picton, and others nearly a decade earlier. Clearly, this statement implies that too much emphasis had been placed on area (the "extinction" side of island biogeography) and too little on isolation (the "colonization" side of island biogeography). It also implies that relatively small fragments may have "worth" despite their small sizes. Relatively small fragments often are not simply random samples of larger habitat units, but rather may represent "special" places that have been left either inadvertently or purposely. For example, R. T. T. Foreman, I. Hanski, E. D. McCoy, and others have shown that relatively small fragments could harbor unusually high population densities of species or disproportionate representations of rare species. Finally, this statement implies that fragmentation cannot proceed indefinitely without severe consequences. Simberloff, for example, has pointed out that "thousands of small fragments, with large aggregate area, will not be expected to allow conservation of many species." If this question—about the dynamics of species extinction—is indeed the only important one remaining, then the information needed to slow the loss of species accompanying area reduction largely is the same information that is needed to predict the loss of species in the first place (refer to the previous section). For example, J. G. Dony, M. E. Soulé, D. Simberloff, and others have recommended identifying target species, determining their minimum viable population sizes (MVPs), and then using known densities to estimate needed area. Unfortunately, even if sound MVPs could be calculated for several target species in a location, the areas required to support those population sizes are

likely to be poorly known, if known at all. This lack of information also plagued earlier proposals for estimating needed area, such as E. D. McCoy's "minimum refuge area," T. E. Lovejoy and D. C. Oren's "minimum critical size," and S. T. A. Pickett and J. N. Thompson's "minimum dynamic area."

C. How Incidence Functions and Nestedness Fit In

Recall that the SLOSS debate was generated largely by one of the early nature reserve design principles: a single intact reserve of a certain area will support more species than a series of individually smaller reserves that are cumulatively of the same area. For this principle to apply universally, the minimal assumptions are that the habitats included on areas of different sizes are more or less uniform, that the population densities of species on areas of different sizes are similar, and that the process of relaxation largely is deterministic. Subsequent ecological research has made it clear that none of these assumptions always holds. However, do these assumptions hold in enough instances or to such a degree that it is possible to know the species composition of various-sized fragments with a high degree of certainty? We shall address two, related, methods developed to address this question.

J. M. Diamond developed "incidence functions" as a tool for determining minimum nature reserve area. The incidence function, J , equals the number of fragments ("islands") of a certain size harboring a certain species divided by the total number of fragments of the same size. Supposedly, the higher the value of J at a particular size, the higher the probability that the species can persist in fragments of that size. E. F. Connor, D. Simberloff, M. Williamson, and others questioned the validity of these conclusions, but, if they do have any validity, even in a general way, then certain patterns of incidence functions could indicate that species disappear from increasingly fragmented habitats in a predictable manner.

B. D. Patterson and W. Atmar developed a sophisticated extension of incidence functions, the "nestedness" of species' geographical distribution. Species' distributions are nested when the species on the most species-poor (and, likely, smallest) fragment comprise a subset of those on the next most species-poor fragment, which, in turn, comprise a subset of those on the next most species-poor fragment, and so on. K. B. Jones and co-workers supplied the first explicit evidence for nested distributions in the mid-1980s, although implicit evidence can be found in papers by N. W. Moore, M. D.

Hooper, R. T. T. Foreman, and others a decade earlier. Jones and co-workers attributed the pattern to selective extinctions in the absence of colonizations, as have most subsequent authors, although D. T. Bolger, M. V. Lomolino, and others have shown that the pattern actually can result from a number of causes. Nestedness could have important implications for nature reserve design. If the species on an archipelago of habitat fragments were a perfect subset of the species in a single large unit of habitat, then the archipelago could never contain more species than the single large unit. Furthermore, if fragments of similar size were to harbor similar suites of species, because species loss with area reduction is deterministic, then the archipelago must contain fewer species than the single large unit. The temptation is great, therefore, to assume that simultaneously significant species-area and nested subset relationships must indicate that smaller fragments have the fewest species, but recent evidence supplied by D. Doak, E. D. McCoy, W. J. Boecklen, and others suggests that this assumption is not a good one.

D. Conclusions

Regardless of the reason for it, poor predictability of the effects of area reduction can stall effective decision making. A good example is the controversy over the amount of species loss accompanying tropical deforestation. For more than 30 years, ecologists have sought "shortcut methods" to substitute for the autecological information that is needed to improve predictability but is so difficult to obtain. To date, they have not been particularly successful. An interesting additional example that involves species-area relationships is the controversy over the amount of species loss accompanying global warming discussed by K. A. McDonald, J. H. Brown, R. W. Skaggs, W. J. Boecklen, T. E. Lawlor, and others. So, we are saddled with a seemingly unresolvable dilemma: we need more information, but we cannot afford to wait to get it. Faced with this dilemma, some biologists, for example R. East and M. Kent, have suggested that we view the species-area relationship as perhaps the best tool available for making conservation decisions and have promoted the idea of retaining large units of habitat as a matter of general course. If one is focusing solely on predicting loss of species with area reduction and refrains from becoming overly specific, then this may be a reasonable strategy. Others, for example C. F. Mason and E. D. McCoy, have suggested that reliance on species-area relationships may lead to undesirable conservation decisions and have promoted a "save-all-the-pieces" strategy. If one is focusing on

forestalling loss of species, then this may be a reasonable strategy (which has been termed SLATS ("several little all too small") by E. D. McCoy and H. R. Mushinsky) for habitats suffering from extreme area reduction and fragmentation. The SLATS strategy is likely to become increasingly relevant for most habitats, because the amount of habitat needed to allow species to persist, let alone to flourish or to evolve, appears to be much larger than humans are willing to grant.

See Also the Following Articles

DIVERSITY, COMMUNITY/REGIONAL LEVEL • HABITAT AND NICHE, CONCEPT OF • ISLAND BIOGEOGRAPHY • METAPOPOPULATIONS • POPULATION DENSITY • POPULATION DIVERSITY, OVERVIEW

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