



MILLENNIUM
GUEST
EDITORIAL
NUMBER 4

Ecology's most general, yet protean¹ pattern: the species-area relationship

Keywords

Area, biogeography, diversity, islands, species-area, species richness.

INTRODUCTION

The species-area relationship is often referred to as the closest thing to a rule in ecology (Schoener, 1976). Along a gradient of ecosystems of increasing size, the numbers of species inhabiting those ecosystems increases; rapidly at first, but then more slowly for the larger ecosystems. The pattern appears to be so common that it would be much more expedient to report the few exceptions (e.g. see Dunn & Loehle, 1988) than the many hundreds, and possibly thousands of studies reporting this pattern for a wide variety of taxa and types of ecosystems. The species-area relationship has been studied for decades and is evidenced by paleontological as well as contemporary patterns (see reviews by McGuinness, 1984; Rosenzweig, 1995; Brown & Lomolino, 1998).

Given the great wealth of research on this long-studied pattern, it might seem that the relationship truly deserves the status of a rule, and that we can confidently use it as a universal tool for understanding and conserving biological diversity. The species-area relationship was, in fact, fundamental to development of MacArthur & Wilson's (1963, 1967) equilibrium theory, which quickly became the paradigm of island biogeography theory and has remained so for the past three decades. As they wrote in their seminal monograph (MacArthur & Wilson, 1967: 8–9), 'theories, like islands, are often reached by stepping stones. The species-area curves are such stepping stones.'

Beyond the general, qualitative pattern (i.e. monotonic, but attenuating increase in richness with area), it has become axiomatic that the actual form of the relationship generally approximates what Preston and others (1962) termed a 'canonical' relationship: a curve which, for isolated ecosystems, is typically approximated by the quantitative model, $S = C A^{z/25}$ (also known as the power, or Arrhenius (1921) model, where S is species richness, and C is a fitted constant that varies in a poorly understood manner among taxa and types of ecosystems). The generality of this 'canonical' relationship is so widely accepted that it is one of the most commonly used tools of conservation biologists attempting to design nature reserves or to predict extinctions during biotic collapse: i.e. the loss of species due to reduction in habitat area (see Shafer, 1990).

Such applications, however, greatly overestimate the generality of the quantitative, canonical form of the species-area relationship. For the power model described above, species richness varies with the value C as well as with the exponent (z). Although z -values tend to be conservative (typically ranging from 0.10 to 0.50), C -values vary by orders of magnitudes. Which values, then, should we use as applied or basic ecologists? While biogeography theory provides some predictions as to how z -values should vary among archipelagoes (see MacArthur & Wilson, 1967: 25–32; see also Schoener, 1976; Connor & McCoy, 1979; Wright, 1981; Sugihara, 1981; Lomolino, 1984, 1989), I am unaware of any comparable body of theory for C -values. To further complicate the issue, while the power model appears to be the most commonly used model to investigate species-area relationships, a semi-log model (the Gleasonian model [Gleason, 1922]; $S = k_0 + k_1 \text{Log (Area)}$) is often used by other ecologists, especially phytogeographers. Unlike the power model, there seems to be no generally accepted, 'canonical', values for parameters of the Gleasonian model.

Perhaps the above comments may seem to some to be just quibbling over methodological approaches. The species-area relationship may, indeed, be one of nature's most general patterns, but we may be using the wrong, or at least an overly simplistic, model. The actual form of the relationship may differ fundamentally from that predicted by conventional models. Regardless of the transformations used and the precise constants and exponents assigned, the power and semi-log models both approximate relatively simple, monotonic relationships. Two critical shortcomings of such models are that they lack an asymptote (for the larger ecosystems) and that they ignore the possibility of what has been termed the small island effect. First, because isolated faunas are ultimately derived from a limited pool of species, the species-area relationship should asymptotically approach or level off at that

¹The term 'protean' refers to Proteus, the Greek Sea God who attended Poseidon and could change his own form at will.

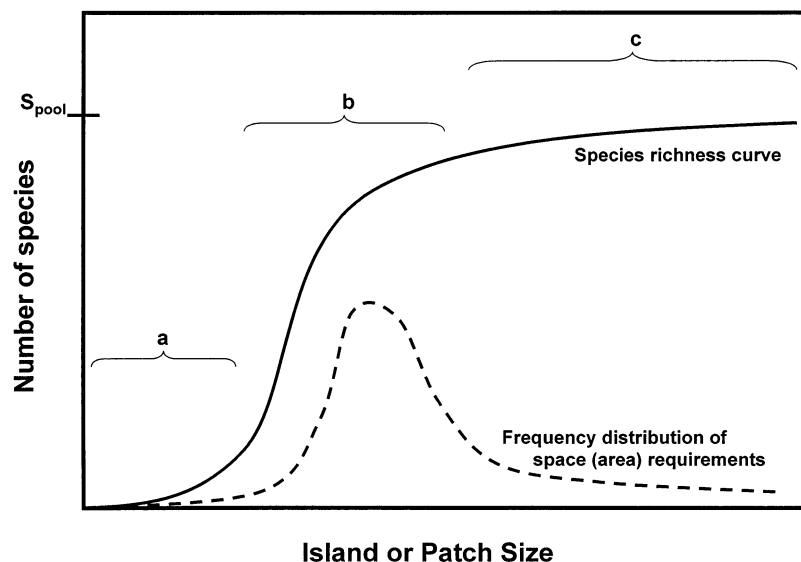


Figure 1 A hypothetical, sigmoidal species-area curve based on the assumption that frequency distributions of population densities, or space and energy requirements of species, are unimodal. Species richness (the accumulative frequency distribution curve, marked by solid line) may appear independent of island area for collections of relatively small islands (i.e. the small island effect; region a) and for collections of the largest islands (region c), where richness should asymptote or level off at that of the species pool (S_{pool}).

maximum value of richness (S_{pool} in Fig. 1). Second, ecologists including MacArthur & Wilson (1967) noted that richness may be independent of island area for collections of relatively small islands (region a in Figs 1 and 2; see studies by Dunn & Loehle, 1988; Wiens, 1962; Whitehead & Jones, 1969; Woodruffe, 1985; Morrison, 1997; see also discussion of the small island effect by Brown & Lomolino, 1998). Granted, the small island effect is not a frequently reported pattern. Yet the paucity of studies reporting this phenomenon may be attributed, at least in part, to sampling biases inherent in most biogeographic studies. That is, we tend to design biogeographic surveys to focus on islands that include an appreciable diversity of species, and then habitually apply one of the above, statistical models (power or semi-log) to summarize the overall pattern. Therefore, either we include very few islands in region a of Figs 1 and 2, or we tend to ignore the tendency for small islands to deviate from the overall trend in log-transformed space.

These biases of survey and analytical protocols do not, however, render the small island effect irrelevant. Most islands or patches of habitat are relatively small (i.e. frequency distributions of patch size should be strongly skewed to the right; Fig. 3), yet most biogeographic studies tend to include a highly disproportionate number of large islands. In contrast, the domain of applied ecology in general, and conservation biology in particular, is largely constrained to collections of small patches of isolated or fragmented habitats. In such cases, community structure may be much more strongly influenced by features other than area, such as natural and anthropogenic disturbance, habitat characteristics within and among patches, patch shape, and degree of isolation (Laurance & Bierregaard, 1997; Noss & Csuti, 1997; Whittaker, 1998; Losos, 1998; Lomolino & Perault, 2000a,b; Perault & Lomolino, 2000).

THE POSSIBLE SIGMOIDAL NATURE OF THE SPECIES-AREA RELATIONSHIP

Taken together, the asymptotic nature of the species-area relationship and the possibility that small island effects are more common than presently perceived argue strongly for a fundamental change in our approach to studying this important relationship. If these phenomena are important, then the species-area relationship should be sigmoidal—with richness remaining relatively low and apparently independent of area for the smaller islands, increasing rapidly to rise through an inflection point for islands of intermediate size, and then asymptotically approaching, or leveling off at the richness of the species pool for the largest islands (Fig. 1). In addition to empirical reasons discussed above, there is an emerging body of theory that also predicts sigmoidal species-area relationships (Lomolino, 1999;

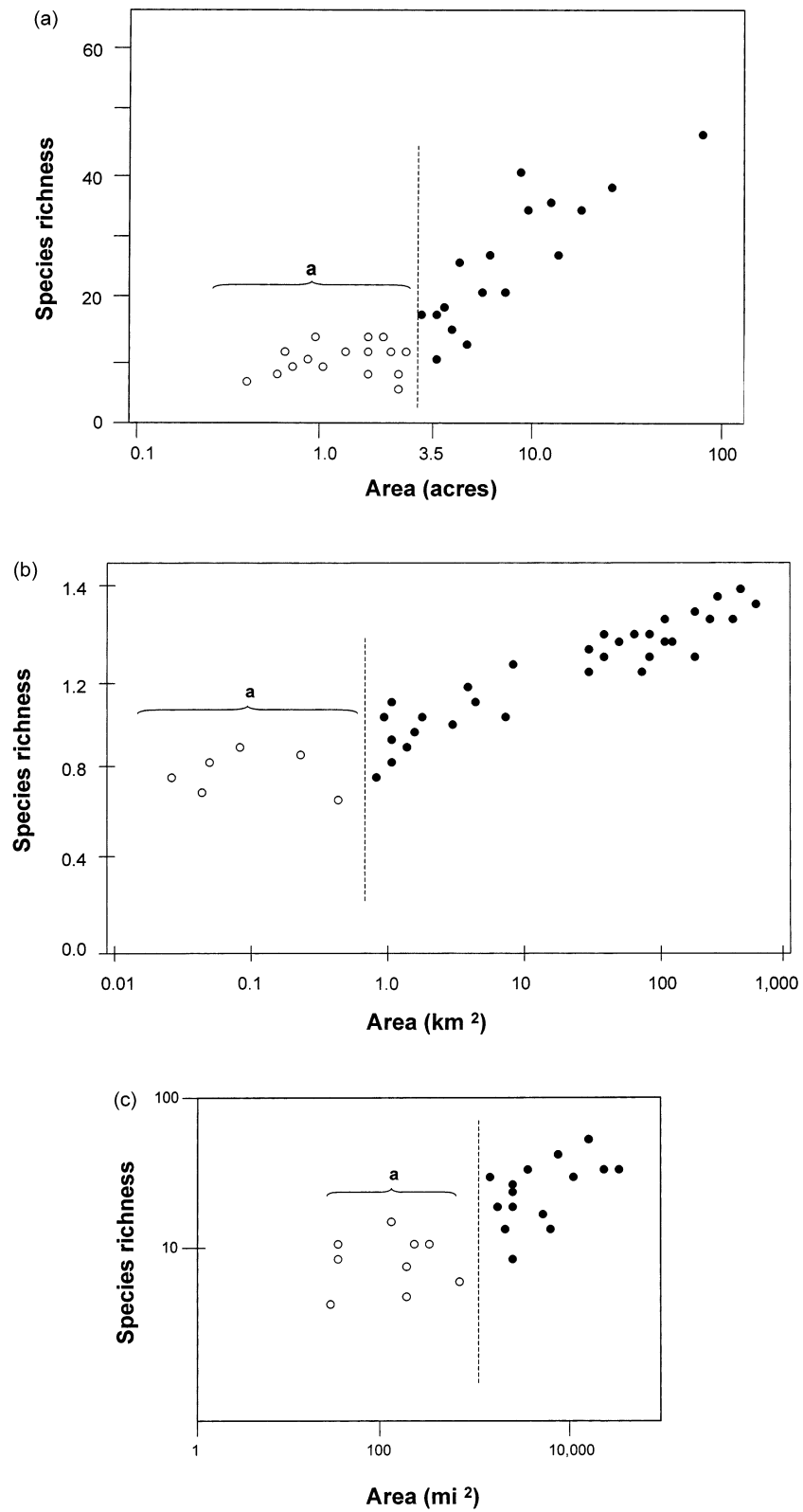


Figure 2 caption on following page

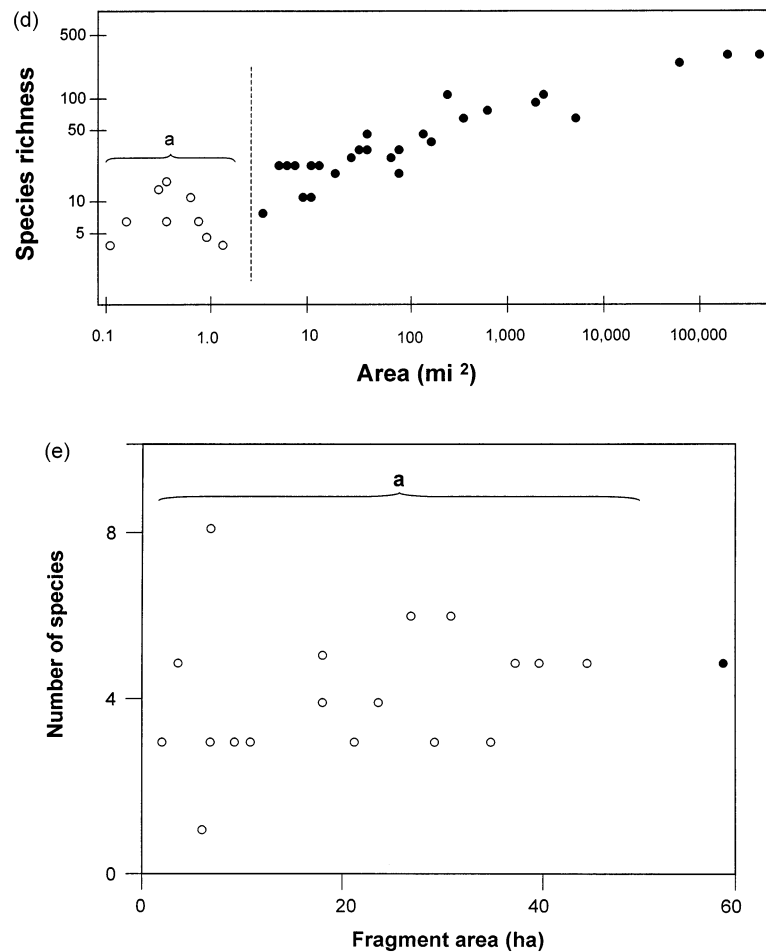


Figure 2 Examples of insular biotas exhibiting what appear to be small island effects (i.e. the lack of a significant species-area relationship for the smaller islands: open circles within range in area delimited by bracket *a*; see Fig. 1). (a) Higher plants of the Kapingamarangi Atoll, Micronesia (MacArthur & Wilson, 1967; after Niering, 1963); (b) terrestrial isopods of the central Aegean islands, Greece (after Sfenthourakis, 1996); (c) ponerine ants of the Moluccan and Melanesian Islands (after Wilson, 1961); (d) land birds of the Malaysian Faunal Region (after Schoener, 1976); (e) non-volant mammals of old-growth, temperate rainforest fragments in Olympic National Forest, Washington, USA (after Lomolino & Perault, 2000b).

Wissel & Maier, 1992; Williams, 1995; Scheiner *et al.*, 2000; Sukhanov, 2000). Whether based on views of deterministic or stochastic community organization, these models share at least one common feature: they assume that frequency distributions of population density, energy requirements, or space use are unimodal. Given this, small island effects may correspond to a range of island sizes where resource levels are insufficient to maintain populations of most species (region *a* in Figs 1 and 2). On these islands, habitat characteristics, episodic disturbances, isolation and interspecific interactions are much more likely to determine how many and which of the few, space conservative species maintain populations (see Losos, 1998; Whittaker, 1998). Such features become less important as island size increases and approaches the space and energy requirements of the modal species (region *b* in Fig. 1). In addition to the five examples of small island effects illustrated in Fig. 2, other apparent cases of such effects include species-area relationships for birds of paramos, sky islands in the Northern Andes, birds and reptiles of the Caribbean islands, plants of Australian islands (see Rosenzweig, 1995: Figs 2.12, 2.6 and 2.7), birds and mammals of the Krakatau and Sunda Shelf islands, and freshwater fish of North American lakes (see Brown & Lomolino, 1998: Figs 13.25 and 13.22). Finally, because frequency distributions of space and energy use tend to be right-skewed (Brown, 1995), increments between space (i.e. area) requirements of the remaining, space and energy intensive species increases along this gradient

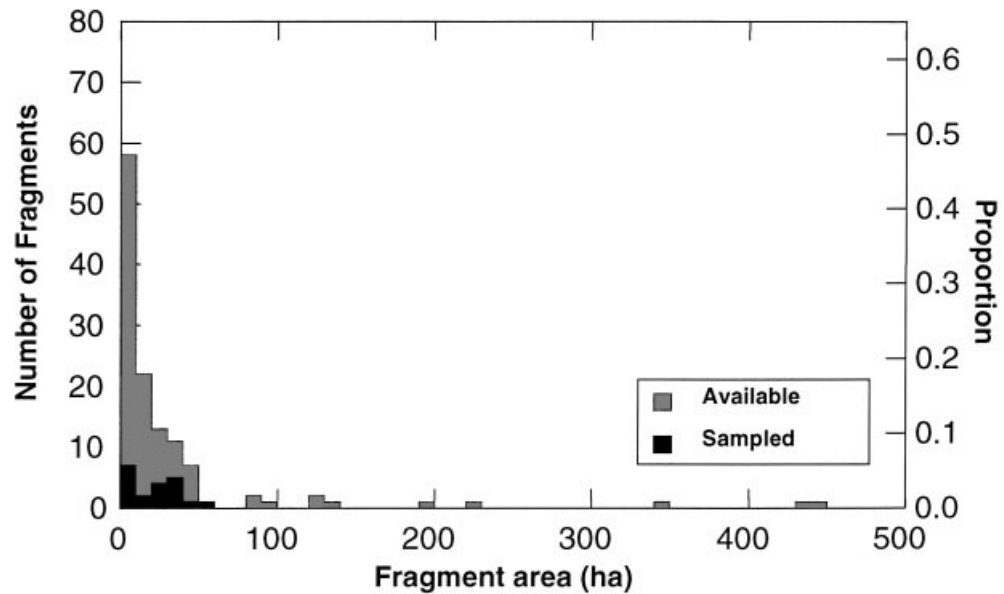


Figure 3 Frequency distribution of sizes of 123 fragments (grey shading) of old-growth, temperate rainforest of the Hoodport District, Olympic National Forest, Washington, USA. Note that the frequency distribution of sites actually surveyed by Lomolino & Perault (2000b; black shading, $N = 20$) did not differ substantially from the distribution of available fragment sizes (see corresponding species-area relationship, including small island effect, in Fig. 2-f). In most biogeographic studies, however, sampling biases (where larger islands or fragments are over-represented) may be common and may lead to under-estimation of the relative importance of small island effects and to an inability to detect the possible, sigmoidal nature of the species-area relationship.

of island size. Thus, the slope of species-area curves should decline (fewer species accumulated for each increment of area) on the larger islands (region *c* in Fig. 1).

The origins of this view of the species-area relationship may be quite old and, ironically, may date back to Preston's initial articulation of the 'canonical' pattern. His ideas on the potential sigmoidal form the species-area relationship are included in the following statements (Preston, 1962: 187).

'This area is at first so small that not until we are within about 9 octaves [a measure of total number of individuals which is also an indirect measures of island area] of the mode ... have we accumulated enough area to correspond to a single species. This is the beginning of the real, finite distribution. As we continue to the right [larger islands] we accumulate species rapidly; then we pass the mode and accumulate them increasingly slowly. Finally we reach a point some 9 octaves to the right of the mode where the remaining area is scarcely enough to hold one more species.'

Later in the same paper Preston (1962: 214–215) refers to what he termed 'Vestal's sigmoidal' curve.

'In 1949 Vestal in the U.S.A. and Archibald in Britain reached the conclusion that in the case of vegetation stands there was a tendency for the species-log area (Gleason) curve to be sigmoid; it began at a low slope, steepened considerably, and then became less steep. I see no reason why the effect should not sometimes exist ... The possibility that such curves may exist can hardly be disputed on theoretical grounds; how often they occur in practices is a matter for observation.'

Thus, in what is certainly one of the seminal studies of the species-area relationship, Preston raised the possibility that the relationship might be sigmoidal and he called for additional empirical studies to evaluate this possibility.

A number of statistical models may be used to analyse sigmoidal patterns, including logistic regression (e.g. see Scheiner *et al.*, 2000) and the extreme-value-function (Williams, 1995, 1996). The sigmoidal-hill function, often used in physiological studies, also may provide some distinct advantages over other models. It includes three parameters, all of which are readily interpretable in this application (S_{\max} = the maximum richness, or asymptote, $Hill_{\text{slope}}$ is a direct measure of the slope of the curve

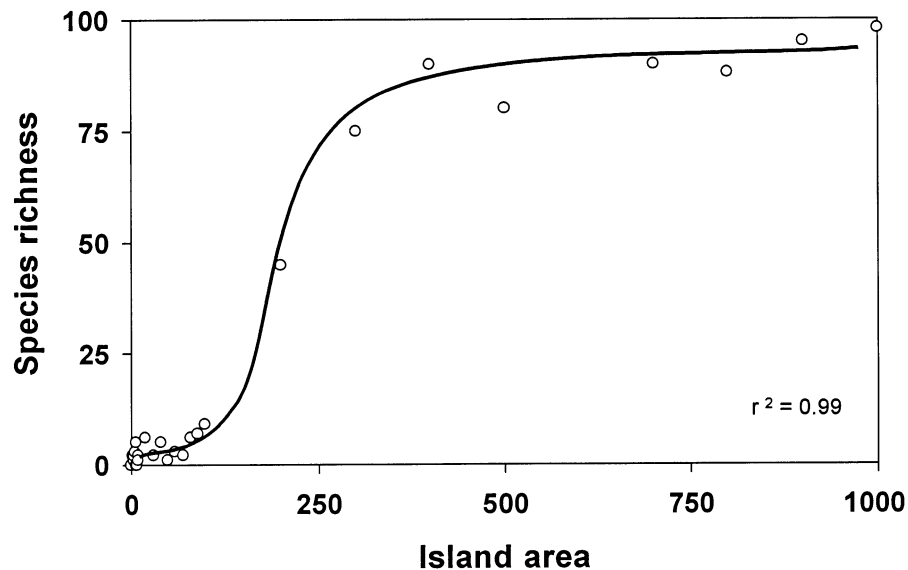


Figure 4 An illustration of applying the sigmoidal hill function to analyse species-area relationships. The pattern for this hypothetical data set ($n = 27$) was analyzed using non-linear, iterative regression (Systat, 1997) and the regression model: $S = S_{\max} / [1 + (\text{Hill}_{\text{slope}})^{\Lambda(\text{Log}(A50/\text{Area}))}]$; where S_{\max} = the maximum richness, or asymptote, $\text{Hill}_{\text{slope}}$ is a direct measure of the slope of the curve through the inflection point, and $A50$ = the area yielding a richness equal to 50% of the maximum richness. Non-linear regression yielded the following estimates for these data: $S_{\max} = 93.23$ ($t = 51.36$, $P < 0.01$), $\text{Hill}_{\text{slope}} = 24.2$ ($t = 3.46$, $P < 0.05$) and $A50 = 199.4$ ($t = 25.5$, $P < 0.01$).

through the inflection point, and $A50$ = the area yielding a richness equal to 50% of the maximum richness; $S = S_{\max} / [1 + (\text{Hill}_{\text{slope}})^{\Lambda(\text{Log}(A50/\text{Area}))}]$. All three of these parameters can be estimated using non-linear, iterative regression methods, or, if S_{\max} is known, it can be entered as a constant in the model before estimating values for $\text{Hill}_{\text{slope}}$ and $A50$. Application of this approach to a hypothetical data set is illustrated in Fig. 4.

A FURTHER COMPLICATION: SPECIES-AREA CURVES OVER LARGE SPATIAL AND TEMPORAL SCALES

The foregoing discussion was based on the assumption that insular communities are largely influenced by stochastic events or deterministic, ecological forces; i.e. the immigration/extinction dynamics envisioned by MacArthur & Wilson (1967). Yet we know that if we consider longer time scales and broader ranges of island area, then insular species richness will also be influenced by *in situ* speciation (see Heaney, 1999). This fact was well appreciated by MacArthur and Wilson and by Eugene Gordon Munroe (1948, 1953) in his original articulation of an equilibrium theory of island biogeography, well over a decade before MacArthur & Wilson's (1963, 1967) independent development of their theory (see Brown & Lomolino, 1998).

'Where speciation is important, as in large islands and continents, the expected size of the fauna is exceeded, but the relationship between area and size of fauna is not lost, but accentuated.' (Munroe, 1953: 53)

Munroe's dissertation focused on Caribbean butterflies, and it still provides an illustrative case study of the intricacies and protean nature of the species-area relationship (see also Davies & Spencer-Smith's [1998] update of Munroe's surveys). Species-area patterns of Caribbean anoles (after Losos, 1998, and Losos, pers. comm., 1999) parallel those of the butterflies (Fig. 5). On smaller islands (arbitrarily chosen as those $< 2,000 \text{ km}^2$), *in situ* speciation should be unimportant and richness should be a function of the interplay between stochastic events such as severe storms (especially on the smallest islands) and immigration/extinction dynamics. Within such ecological temporal and spatial scales, the species-area relationship should be a curvilinear, and possibly sigmoidal relationship for reasons discussed above.

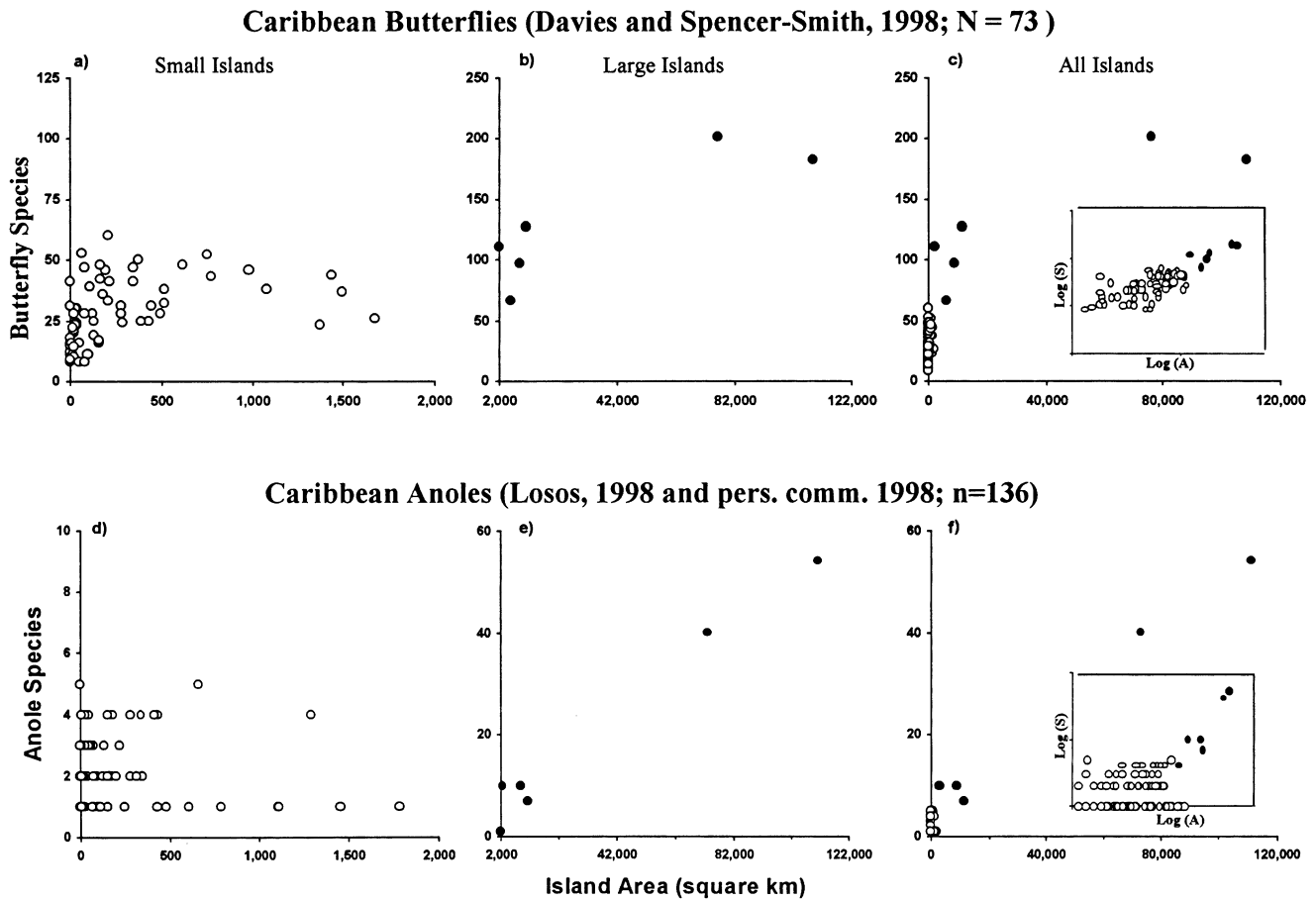


Figure 5 An illustration of the scale-dependent nature of species-area curves for Caribbean butterflies and anoles. Species-area relationships vary in a similar manner for these faunas, but differ substantially over different ranges of island area. Collections of smaller islands (graphs a and d) appear to exhibit small island effects. The conventional approach to graph and analyze these patterns in log-transformed space (insets of c and e) masks some of the more interesting features of the species-area relationship (see Fig. 6).

As we consider larger (and more isolated) islands, however, the species-area relationship should be deflected upward—or in Munroe's terms, the relationship should be 'accentuated' by the effects of *in situ* speciation. The differences between the two curves should represent the contribution of endemic species to total richness of these insular faunas (Fig. 5, dashed versus solid lines for insular communities primarily influenced by ecological, or by both ecological and evolutionary processes, respectively).

Note, however, that these potentially insightful, scale-dependent features of the species-area relationship are rendered undetectable in log-transformed space (Fig. 5 c and f, insets); i.e. the conventional approach employed by most biogeographic studies to simplify and linearize the species-area relationship. The loss of biologically meaningful and heuristically valuable information should be obvious.

CONCLUSION

These questions on the fundamental nature of the species-area relationship suggest several important lines of research for both basic and applied ecologists. First, they call for a reassessment of the potential importance and generality of the small island effect and the influence of scale on the nature of the species-area relationship (see Martin, 1981). While this may in some cases require altering the design of biogeographic surveys (to include a broader range of island area and greater representation of small islands), it is likely that sufficient information is available to allow a re-assessment and meta-analysis based on existing data sets. Second, existing data sets also can be analysed to compare the efficacy and heuristic value of statistical models based on power, sigmoidal or other forms of species-area curves

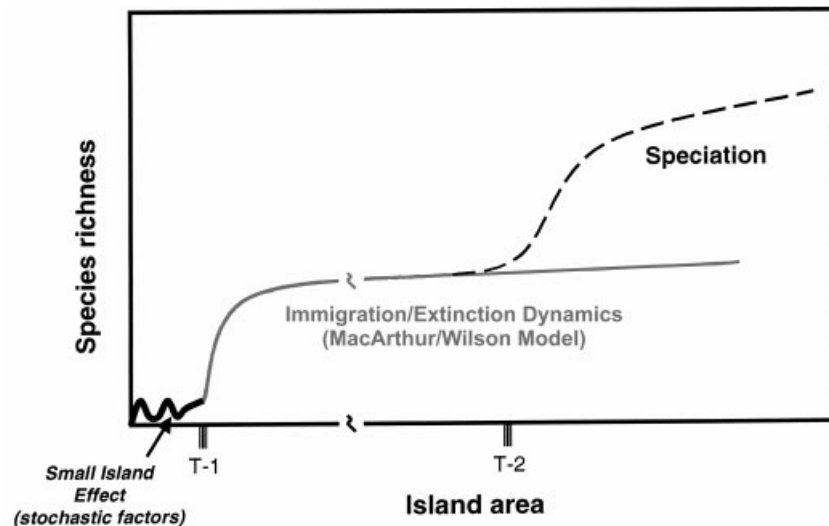


Figure 6 The scale-dependent nature of the species-area relationship may best be studied by focusing on thresholds which delineate ranges of area where, (1) richness seems to be independent of area and is largely determined by stochastic factors, (area < Threshold 1), and (2) species richness is a function of immigration/extinction dynamics as envisioned by MacArthur & Wilson (1967); range in area between Thresholds 1 and 2, or (3) islands large enough to allow in situ speciation (i.e. those beyond Threshold 2).

(e.g. Scheiner *et al.*, 1999; He & Legendre, 1996). Third, such analyses can be used to search for central tendencies in parameters of these models (e.g. C , A_{50} , and $Hill_{slope}$), and to investigate whether these parameters vary in any regular manner among taxa, functional groups or ecosystem types, or across different spatial scales.

Alternatively, it may prove more instructive to abandon the more traditional exercise of comparing partial slopes (i.e. z -values) of species-area curves and instead compare asymptotes of species richness (at ecological scales) or key thresholds of island area. Over a sufficiently broad range of island areas, we may detect at least two such thresholds (Fig. 6).

- (1) One corresponding to the upper limit of small island effects, below which episodic disturbances and other stochastic events may play a major role in determining species richness (S appears to be largely independent of area until this threshold is exceeded).
- (2) A second threshold delineating the area beyond which islands are large enough for in situ speciation to occur. Between thresholds 1 and 2, insular species richness is largely determined by immigration/extinction dynamics within ecological time scales. As island area increases beyond Threshold 2, the relative importance of evolutionary processes increases, while immigration/extinction dynamics become less important determinants of inter-island differences in species richness (see Wilson, 1969 and models by Heaney, 1999).

Future studies that assess and compare such thresholds among taxa or archipelagoes are likely to provide some fundamental insights into the forces structuring isolated and fragmented ecosystems over a broad range of temporal and spatial scales. What was thought to be most general pattern in ecology and biogeography, one studied for over two centuries, may prove to be much more complex than we have appreciated. This complexity may be disheartening to some, rendering simple analyses and comparisons of one statistical parameter (z), highly suspect. Others, however, will likely embrace this complexity as a more accurate reflection of the complexity of nature and the combined, scale-dependent influences of stochastic factors, immigration and extinction dynamics, and speciation.

ACKNOWLEDGMENTS

During the preparation of this manuscript I received funds from National Science Foundation grants (DEB-9322699, DEB-9707204 and DEB 9622137). J. H. Brown, M. L. Falcon, L. Heaney, J. Losos,

M. Fuller, N. Gotelli, M. Kaspari, D. R. Perault, G. Smith and L. S. Walker, R. J. Whittaker and M. Willig provided useful comments on the concepts discussed here.

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