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Six types of species-area curves

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ABSTRACT

Macroecological studies infer ecological processes based on observed patterns. An often used measure of pattern is the species-area curve. Insufficient attention has been paid to the variety of methods used to construct those curves. There are six different methods based on different combinations of: (1) the pattern of quadrats or areas sampled (nested, contiguous, noncontiguous, or island); (2) whether successively larger areas are constructed in a spatially explicit fashion or not; and (3) whether the curve is constructed from single values or mean values. The resulting six types of curves differ in their shapes, how diversity is encapsulated, and the scales encompassed. Inventory diversity (α) can either represent a single

value or a mean value, creating a difference in the focus of the measure. Differentiation diversity (β) can vary in the extent encompassed, and thus the spatial scale, depending on the pattern of quadrat placement. Species-area curves are used for a variety of purposes: extrapolation, setting a common grain, and hypothesis testing. The six types of curves differ in how they are used or interpreted in these contexts. A failure to recognize these differences can result in improper conclusions. Further work is needed to understand the sampling and measurement properties of the different types of species-area curves.

Key words differentiation diversity, extent, focus, grain, inventory diversity, macroecology, scale, species-area curve.

INTRODUCTION

Macroecology can be defined as the study of ecological patterns and processes at scales of space and time beyond the reach of manipulative experiments. This methodological definition highlights the fact that macroecology relies on observational or inferential hypothesis tests. We start with pattern and try to infer the responsible mechanism(s). Thus, it is critical that we understand the patterns that we are observing.

A fundamental pattern is the way in which the total number of species increases as the sampled area increases. Recognition of this pattern dates to the work of de Candolle (1855) and Jaccard (1901, 1908), and was formalized subsequently as the species-area curve (Arrhenius, 1921; Gleason, 1922; Cain, 1938; McIntosh, 1985). The increase in number of species comes about for two reasons. First, as more individuals are sampled, the chance of encountering additional species increases, especially if species are not randomly distributed. Second, a larger area is likely to be more environmentally heterogeneous, thus containing additional species that differ in their niches.

This increase of species number with area has been called one of the few laws of ecology (Schoener, 1976), making species-

area curves a prime measure of ecological pattern. Ecologists tend to speak of *the* species-area curve, even though there are a variety of types. My goal is to define six types of curves and to discuss how they measure different aspects of diversity. The issues raised in this paper are not new; many were considered during the original development of the species-area literature. Collecting these issues in one place, resurrecting issues long dormant, and providing a typology for discussion, will advance our ability to match pattern and process accurately. Much work is needed to enable us to go from the data embodied in a species-area curve to an understanding of underlying causal mechanisms. A critical first step is to understand both the biological and statistical underpinnings of species-area curves prior to using them to interpret and test macroecological theories.

Six types of curves

Six types of species-area curves can be defined by the characteristics of sampling (Fig. 1) combined with the method of analysis (Table 1). A distinguishing feature of a Type I curve is that each data point is based on a single measurement for a given size. In contrast, Type II and Type III curves are constructed by estimating the mean diversity for a given area,

Table 1 Six types of species-area curves. They differ in their method of construction and their resultant properties

Type	Method of construction			Properties			
	Sampling scheme	Spatially explicit	Analysis method	Shape	Nondecreasing	Function of†	Extent
I	Nested	Yes	Single points	Stairstep	Yes	α and β	= sampled area
IIA	Contiguous	Yes	Means	Smooth curve	Yes	$\bar{\alpha}$ and $\bar{\beta}$	= sampled area
IIB	Contiguous	No	Means	Smooth curve	Yes	$\bar{\alpha}$ and $\{\bar{\beta}\}$	= sampled area
IIIA	Non-contiguous	Yes	Means	Smooth curve	Yes	$\bar{\alpha}$ and $\bar{\beta}^*$	> sampled area
IIIB	Non-contiguous	No	Means	Smooth curve	Yes	$\bar{\alpha}$ and $\{\bar{\beta}^*\}$	> sampled area
IV	Island	No	Single points	Smooth curve	Not necessarily	$\bar{\alpha}^*$ and $\bar{\beta}^*$	> sampled area

† A bar over a symbol indicates that the measure is averaged over the sample; brackets indicate that the measure is averaged over all distances; a plus indicates that the effect includes the area between the quadrats; an asterisk indicates that the averaging also includes variation in the pattern of environmental heterogeneity.

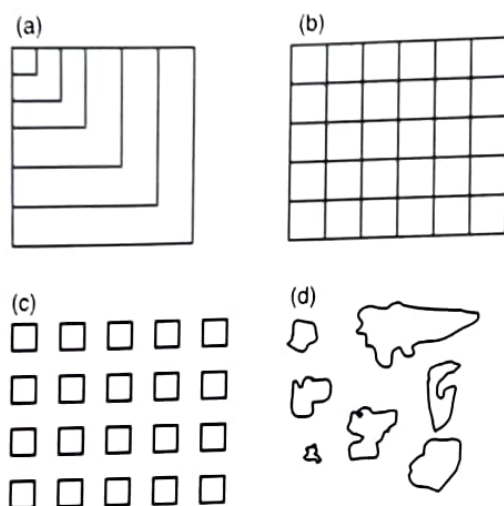


Fig. 1 Species-area curves can be built from four general sampling schemes: (a) strictly nested quadrats (Type I curves); (b) quadrats arrayed in a contiguous grid (Type II curves); (c) quadrats arrayed in a regular but noncontiguous grid (Type III curves); or (d) areas of varying size, often islands (Type IV curves).

which can be done in two ways. Spatially explicit methods retain information on the spatial arrangement of quadrats (Type IIA and IIIA curves). The alternative is to ignore spatial information (Type IIB and IIIB curves). The spatially explicit method begins by calculating the mean diversity for each quadrat; this provides the first data point — the mean number of species in an area of 1 unit. Next, determine the diversity of all combinations of adjacent quadrats and again calculate the mean — the mean number of species in an area of 2 units. Do this again for triplets, quadruplets and so forth. [To keep matters of geometry simple, we might specify that the set

must be as compact as possible, or only use square sets (1, 4, 9, 16 ...).] For Type IIIA curves, one would use the nearest quadrats, rather than adjacent ones. Alternatively, ignore spatial arrangement. Again begin with single quadrats and go on to pairs, triplets, and so forth. But now, all possible pairs, triplets or quadruplets are used, not only adjacent quadrats. This latter method is employed by two commonly used software packages: PC-ORD (McCune & Mefford, 1997) and EstimateS (Colwell, 1997).

A Type IV curve, like a Type I curve, is built from single data points. The difference is that each data point is from a sample of a unique area. It is typically constructed from samples of islands or island-like habitats (e.g. lakes, mountain tops, isolated forest stands, continents). The Type IV curve is associated most often with oceanic islands (e.g. Darlington, 1943) due to its promotion by MacArthur & Wilson (1967).

The use of all curve types goes back to the earliest discussions of the species-area relationship. For example, Braun-Blanquet (1932) and Cain (1938) compare the efficiencies of Type I and Type IV curves for determining the minimum area needed for sampling a community. Gleason (1922) raised the issue of whether a Type IIB curve or a Type IIIB curve provides the best method for estimating the total species richness of a community (see Palmer & White, 1994 for a recent example). The use of different types of curves has changed over time. In the 1930s and 1940s, species-area curves were primarily the province of phytosociology (plant community ecology) where either Type I curves or Type IIIB curves were used to determine the optimal quadrat size or sampling area (e.g. Cain, 1934, 1935). Currently, studies primarily focus on assessing the effects of area on diversity and are dominated by Type IV curves. Examples of nearly all types of curves can be found both in the early and contemporary literature, except for the Type IIIA curve, for which I was unable to find any examples.

Although the six curves define the range of types, ecologists have employed a number of variants. For example, to determine

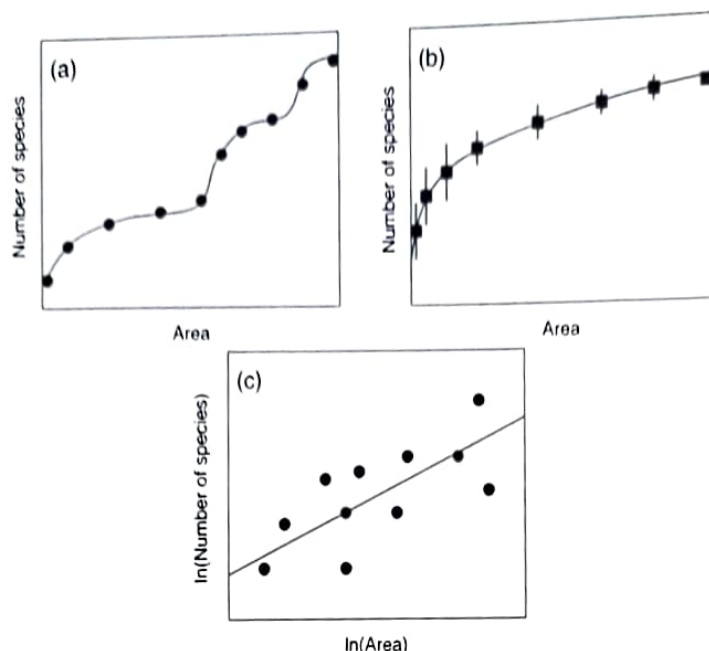


Fig. 2 (a) A Type I species-area curve may form an irregular staircase pattern. Within a community, the rate of increase in species richness decreases as the area increases. When a community boundary is crossed, however, the number of species found will once again rise rapidly. At a given area, each point represents a single measure. (b) A Type II or Type III curve will always form a smoothly rising pattern. At a given area, each point represents multiple measures, with the curve based on the mean of those measures and around which will be some variation. (c) A Type IV curve is typically calculated as a linear regression on a log-log scale. Each point represents a single measure.

optimal quadrat size, Cain (1934) employed a system of averaged Type I curves — multiple sets of nested quadrats. In other cases, ecologists have created Type IIA curves, but only calculated diversity for a subset of all possible combinations.

MEASUREMENT PROPERTIES

The shape of the curve

With regard to shape, a Type I curve differs from the others in potentially being an irregular staircase (Fig. 2). Consider a situation where a sample begins in a meadow and eventually expands to include an adjacent forest. Initially, the number of species will rise rapidly. But as more and more of the meadow is captured in the ever-growing plot, the number of additional species found will diminish. At some point, it is likely that one will stop finding additional species, and the curve will level off. If one expands the sampling into the forest abutting the meadow, one will find a whole new suite of species. The species-area curve will again rise rapidly with increasing area until, once again, it levels off as most of the forest gets sampled. This staircase pattern will be repeated each time one crosses a new community boundary. A Type I curve,

though, could be a smooth function if the grain of environmental heterogeneity was smaller than the areal sampling steps. In contrast, all of the other curves are always smooth functions.

The six types differ in whether they are nondecreasing. Because Types I, II and III are all built using larger and larger combinations of the same areas, they must be nondecreasing. In contrast, a Type IV curve is under no such constraint. It is possible for a larger island to contain fewer species than a smaller island, and actual samples show substantial variation. As far as I am aware, no one has attempted to fit a decreasing curve (e.g. quadratic) to island data. Although ecologists always fit Type IV curves using nondecreasing functions, a decreasing curve is at least theoretically possible.

The best mathematical function for the shape of the species-area curve has been debated over the years (He & Legendre, 1996; Tjørve, 2003). The three most widely used candidates are:

the exponential curve (Gleason, 1922, 1925),

$$S = z \ln(A) + c$$

the power curve (Arrhenius, 1921, 1923a,b),

$$\ln(S) = z \ln(A) + c$$

and the logistic curve (Archibald, 1949),

$$S = \frac{b}{c + A^{-z}}$$

where S is the number of species, A is the area, and b , c , and z are constants.

These three functions make different assumptions about the relationship of species number and area. Both the exponential and power functions result in curves that continue to rise indefinitely. The logistic function, on the other hand, eventually reaches a plateau. The interpretation of the parameters of the exponential and power functions is straightforward; z is the slope and c is the intercept of the line on semilog and log-log representations of the relationship, respectively. In contrast, the interpretation of the parameters for the logistic function is less simple; b is the elevation of the curve, while c and z together affect the curvature, the rate at which species accumulate with area. The asymptote of the curve is b/c , which represents the total species richness in the sampled extent. Other functions are possible. For example, Williams (1995) proposed an extreme-value function model as an alternative to the power curve. Tjørve (2003) presents a comprehensive survey of proposed functions, including six convex functions such as the exponential and power functions, and eight sigmoidal functions such as the logistic and extreme-value functions.

Although the issue of the relationship between scale and curve shape was raised as far back as Arrhenius (1923a), tests of the shape of a curve are not commonly done (Tjørve, 2003). There was a long debate about whether Type IV curves were exponential or power functions (Gleason, 1922; Arrhenius, 1923a; Preston, 1962a; Connor & McCoy, 1979; Sugihara, 1981; McGuinness, 1984). Based on Preston's (1962) derivation of a power function from a log-normal species abundance distribution, the current consensus is that the power function is the best fit (e.g. Sugihara, 1981; Wissel & Maier, 1992; Rosenzweig, 1995), so that a power function is usually assumed in an uncritical fashion. A notable exception is He & Legendre (1996) who showed for a 50-ha forest in Malaysia that the shape of a Type I curve differed as a function of the extent of the sample. At larger scales, Rey Benayas & Scheiner (2002) concluded that the logistic function provided the best fit for 93 Iberian landscapes that ranged in size from 100 km² to 5000 km². Tjørve (2003) suggests that other sigmoidal functions, such as the cumulative Weibull, may be more appropriate for a Type IV curve.

Diversity components

The six curves differ in how they measure two diversity components: inventory diversity (the diversity of species contained

within a unit) and differentiation diversity (the way in which those species are grouped into subunits) (Whittaker, 1977). In a spatial context, differentiation diversity is the extent to which species composition changes from one place to another; it is a function of nonrandom dispersion of species due to both localized dispersal and environmental heterogeneity. For simplicity I use α diversity and β diversity as synonyms for inventory diversity and differentiation diversity, recognizing that both often have specific scale connotations that I am ignoring (Whittaker *et al.*, 2001). A third diversity component, pattern diversity (which is the relative arrangement of subunits within an ecological unit; Scheiner, 1992), is not considered here because the relationship between the shape of a species-area curve and this component has not been determined.

All four types of species-area curves are functions of α and β diversity, although in different ways. If an exponential or power function is fit to a Type I curve, the intercept (c) measures α diversity, and the slope (z) measures β diversity (MacArthur, 1965). Although α diversity is often equated with the intercept of a species-area curve, I emphasize that no particular spatial scale is privileged and inventory diversity can be measured for any area. The ecological interpretation of the parameters of other functions is still to be worked out (Tjørve, 2003).

Type II, III and IV curves each measure the average inventory diversity (α) of the entire sample, and involve an averaging of differentiation diversity (β). This averaging is easiest to see with regard to a Type IIA curve. One can conceive this curve as the average of a series of regression lines, each based on a particular Type I curve. The result is an average slope (β). A Type IIB curve adds yet another form of averaging, the difference in diversity among quadrats averaged over all distances, which I have notated as $[\beta]$. For example, $[\beta]$ would be a function of how different the environment is from place to place — and how those environmental differences result in species composition differences — for all possible distances between places.

Type III curves differ from Type II curves in that the distance effect that creates β diversity has two parts: differences in species composition among areas sampled, as well as differences due to the distances between the quadrats. That is, β diversity is a function of the entire extent of the sample, which is larger than just the sum of the areas of the quadrats; this effect I notate as β' .

A Type IV curve is a function of both α and β diversity in a way that contains elements of both a Type I curve (a single effect) and a Type II or Type III curve (an average effect). They are single effects under the assumption that the pattern of environmental heterogeneity is the same on all islands. Otherwise, they are an average of the patterns on each island. This averaging differs from the averaging of Type II and Type III curves because the latter are averaging over portions within a

single pattern. This difference is notated as α^* and β^* . All of these different notations are not simply to add to ecology's terminological proliferation; they remind us that each curve is measuring something different.

There are a large variety of measures of inventory and differentiation diversity (Magurran, 1988; Gurevitch *et al.*, 2002). All species-area curves measure inventory diversity as species density, the number of species per unit area, thus explicitly indicating the scale of measurement. Scale is often not made explicit in diversity measures (Whittaker *et al.*, 2001).

In contrast, the types of curves vary in which form of differentiation diversity each measures. Whittaker (1977) delineated two ways for measuring differentiation diversity: species turnover along a gradient and mean similarity (or dissimilarity) among a set of samples. As indicated above, the slope of a species-area curve has been proposed as a measure of differentiation diversity. Mean similarity most closely relates to a slope from a Type IIB or IIIB curve, because both are averaged across all combinations of quadrats and distances. In contrast, gradient turnover most closely relates to a slope from a Type I, IIA or IIIA curve, because all include a spatially explicit (distance) component. These analogies are only approximate and additional work must determine the equivalences.

Scale components

These differences among the types of curves are partially a function of the scales encompassed by a species-area curve. Scale has three components: grain, focus and extent (Palmer & White, 1994; Scheiner *et al.*, 2000; Whittaker *et al.*, 2001). Grain is the size of the common analytical unit. Focus is the area or inference space represented by each data point. For example, it may represent the scale at which the grains are aggregated or the scale at which a mean is calculated. Although the focus of an analysis may be larger than the grain, it can never be smaller. Extent is the scale at which the entire set of sample-units is analysed.

For all types of curves, the grain is the designated area associated with a measure of diversity, i.e. the point along the abscissa one is considering. The curves differ, though, with respect to their focus and extent. With regard to extent, for Type I and Type II curves the extent equals the total sampled area, and for Type III and Type IV curves the extent is the entire area over which the quadrats or islands are dispersed. With regard to focus, the types again differ. For a Type I curve, the focus always equals the grain because the number of species estimated for a given area is based on a single sample of that size. For all other types of curves, the number of species estimated for a given area is averaged over all samples. Thus, the focus equals the entire extent of the sample. In this fashion, the placement of spaced quadrats (Fig. 1c) can be used to manipulate focus. It is even possible for the focus to

be greater than the extent, if the sampled area is meant to be representative of a larger area. For all types of curves, the focus of β diversity is always equal to or greater than the extent, as it is a function of the entire sample.

WHAT THEY ARE USED FOR

Species-area curves have been used for a variety of purposes, including extrapolation, establishing a common grain, and hypothesis testing. For example, a current debate concerns the likely continental and global patterns of diversity resulting from the human-induced rise in species migration and invasion (McKinney, 1998; Rosenzweig, 2001, 2002; Collins *et al.*, 2002). The debate uses Type IV curves to extrapolate diversity patterns from continental to global scales.

Attempts at combining data from different surveys requires establishing a common grain or set of grains for analysis (Scheiner *et al.*, 2000). Type II and III curves are ideal for such usage because they average across samples. One just has to keep in mind that the focus differs from the grain, so even when the grains are standardized, the foci may still differ. Diversity patterns can vary as a function of both grain and focus (Scheiner & Jones, 2002). Rey Benayas & Scheiner (2002) provide an example of the importance of keeping track of focus when interpreting patterns of diversity. Type III curves can be used to manipulate focus, either *a posteriori* by varying which quadrats and their spacing one includes in a calculation, or *a priori* by determining the best sample spacing to address a particular question.

Much effort has been directed towards determining the best size and shape of a quadrat (Cain, 1938; Penfound, 1945; Johnson & Hixon, 1952; Bormann, 1953; Bourdeau, 1953; Kershaw, 1973). In contrast, much less thought has been given to the spacing of quadrats, although the issue goes back to Gleason (1922) and Cain (1936). Scattered quadrats generally will produce a curve that bows upward (lies above), compared to curves based on nested quadrats because at equal sampling areas, a dispersed set of samples is likely to encounter more species than contiguous samples (Gleason, 1922; Palmer & White, 1994). That is, 100 1-m² quadrats dispersed across 1 ha will be likely to contain more species than a single 10 × 10-m² quadrat because usually species are not distributed uniformly in space. Clumping can occur due to localized dispersal or because the environment is heterogeneous. Scattered quadrats are more likely to encounter more clumps or types of environments and, thus, more species than would a single quadrat of equal area. The magnitude of this effect depends on the geospatial characteristics of clumping.

Species-area curves can be used to test hypotheses about which processes are responsible for patterns of diversity by facilitating comparisons measured at different spatial scales (Scheiner *et al.*, 2000). For example, Rey Benayas & Scheiner (2002) in a study of Iberian plant diversity used species-area

curves to estimate species richness at two scales: 100-m² and entire landscapes. They found that species richness at the local scale was negatively correlated with seasonality in precipitation, but not at the landscape scale and concluded that limitations of adaptation to harsh environments likely had a greater effect at smaller spatial scales. MacArthur & Wilson (1967) argued that the greater slope of Type IV curves for oceanic islands as compared to continents indicates that the diversity of each is differentially controlled by the rates of migration and the size of species pools.

The properties of species-area curves have been predicted from models of community processes (e.g. Preston, 1962a,b; Coleman, 1981; Caswell & Cohen, 1993; He & Legendre, 2002; Plotkin & Muller-Landau, 2002). Those efforts begin with an analytic model of species dispersal and interaction and then predict the relationship between species and area. An alternative approach is to explore the properties of the different types of curves through simulations which vary in their patterns of species dispersal and interaction. In testing any model, it is important that the sampling scheme mirrors the model assumptions. For example, Caswell & Cohen (1993) assume a metapopulation patch structure with no spatial component. This structure is most closely matched by a Type IIIB curve. In contrast, Plotkin & Muller-Landau (2002) assume a contiguous spatial structure that is most closely matched by a Type IIA curve. And, of course, island biogeography theory (MacArthur & Wilson, 1967; Wissel & Maier, 1992) matches a Type IV curve. Similarly, Coleman (1981) proposed a model of random placement of individuals on islands, which is also matched by a Type IV curve (Coleman *et al.*, 1982). Much more work is necessary to understand the sampling properties of the different types of species-area curves and how they reflect underlying ecological processes.

OTHER KINDS OF CURVES

Another class of species diversity curves, accumulation or rarefaction curves, bears a resemblance to species-area curves (e.g. Sanders, 1968; Hurlbert, 1971). These curves are constructed using the number of observed species as a function of the number of sampled individuals, rather than the sampled area. They can be based on a sample from a single time period or constructed from repeated sampling over time. Thus, diversity can accumulate in samples in space or time. How samples over space and time compare is unclear (Preston, 1962a,b; Rosenzweig, 1995; Condit *et al.*, 1996). Many of the same issues raised in this paper about species-area curves also apply to these curves. For example, one can vary the temporal spacing (focus) and extent. While single-sample curves are typically generated by a complete randomization of the sampled individuals (similar to Type IIB and Type IIIB curves), time accumulation curves are often based on a single time course (similar to a Type I curve). An accumulation curve

could be constructed by randomizing over time, although I am not aware of any examples. See Rosenzweig (1995) for a more detailed discussion of accumulation and rarefaction curves.

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BIOSKETCH

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