

Species richness, species–area curves and Simpson’s paradox

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ABSTRACT

A key issue in ecology is how patterns of species diversity differ as a function of scale. The scaling function is the species–area curve. The form of the species–area curve results from patterns of environmental heterogeneity and species dispersal, and may be system-specific. A central concern is how, for a given set of species, the species–area curve varies with respect to a third variable, such as latitude or productivity. Critical is whether the relationship is scale-invariant (i.e. the species–area curves for different levels of the third variable are parallel), rank-invariant (i.e. the curves are non-parallel, but non-crossing within the scales of interest) or neither, in which case the qualitative relationship is scale-dependent. This recognition is critical for the development and testing of theories explaining patterns of species richness because different theories have mechanistic bases at different scales of action. Scale includes four attributes: sample-unit, grain, focus and extent. Focus is newly defined here. Distinguishing among these attributes is a key step in identifying the probable scale(s) at which ecological processes determine patterns.

Keywords: combining data, productivity, scale, species–area curve, species diversity, species richness.

INTRODUCTION

A key issue in ecology is how patterns of species diversity differ as a function of scale (Brown, 1995; Rosenzweig, 1995; Gaston, 1996). For example, Waide *et al.* (1999) show that the relationship between species richness and productivity changes depending on the spatial scale over which these variables are measured. Such scale dependency can reveal the operation of important processes that need to be incorporated into any general theory explaining relationships involving species diversity (e.g. Palmer and White, 1994; Pastor

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et al., 1996). In this paper, we explore three issues necessary to examine patterns of species richness and some potential controlling variable, using productivity as our exemplar. (1) How do issues of scale arise as a consequence of the species–area relationship? (2) When is the species–area relationship scale invariant with respect to a third variable? (3) What are the components of scale and how do they affect our view of ecological processes?

SPECIES–AREA RELATIONSHIPS

If we wish to relate species richness (the number of species observed within a specified area) to some environmental factor, especially if we are comparing or combining data from a variety of sources, we need a function that standardizes estimates of species richness to a common scale. This scaling function is a species–area curve. The species–area relationship is a consequence of two independent phenomena. The total number of individuals increases with area, leading to an increased probability of encountering more species with larger areas, even in a uniform environment (Coleman *et al.*, 1982; Palmer and White, 1994; Rosenzweig, 1995). If this were the only factor affecting the rate of accumulating species, and if the number of individuals sampled were large enough, then the species–area curve would approach an asymptote at the total number of species in the species pool. The asymptote requires that, at some spatial scale, species distributions are sufficiently mixed and rare species are sufficiently abundant that all species will be encountered before the entire space is sampled. Although for terrestrial systems, especially for plants, this curve is plotted with respect to area, it could be plotted with regard to other measures of sampling effort, such as number of net tows for zooplankton.

The second factor that affects the species–area relationship is environmental heterogeneity. As area increases, more types of environments are likely to be encountered. If species are non-uniformly distributed with regard to environments, then the number of species encountered will increase with area. In this instance, the species–area curve will reach an asymptote only if the number of environments reaches an asymptote at some spatial scale. Or, put another way, an asymptote requires that, at some scale, environmental types are sufficiently mixed and abundant such that all types will be encountered before the entire space is sampled.

The likelihood of both factors leading to asymptotic species–area curves depends on the particular characteristics of the ecological system of interest and the way in which it is sampled (e.g. nested quadrats *vs* dispersed quadrats). Species mixing in a uniform environment may occur within a single community. However, at biome to continental scales, such mixing is less likely because biogeographic and evolutionary processes – such as speciation events, large-scale movements due to climate change, dispersal barriers, and so on – continually lead to non-equilibrial distributions of species. With regard to environmental heterogeneity, no general answer is possible because the distribution of habitats is system-specific. For example, in the open water of a lake, heterogeneity is small and environmental types are likely to be well-mixed throughout the entire lake (e.g. Dodson *et al.*, in press). Conversely, a mountainous area has a complex pattern of environmental heterogeneity as a consequence of slope, aspect, elevation and soil type. A species–area curve for terrestrial plants in this system may never attain an asymptote given the usual constraints of sampling. Thus, issues of spatial scale must be resolved within the spatial context of each system under consideration.

SCALE AND INVARIANCE

Regardless of the shapes of species–area curves, they can provide a quantitative means to compare different systems at a common sampling scale; for example, by comparing species richness among systems at an adjusted area of 10 m². In addition to providing a standardized measure of species richness, species–area curves also reflect the way that diversity is structured spatially and how environmental variables affect richness at different spatial scales. If scale ‘matters’, then observed relationships between richness and environmental factors, say productivity, will vary depending on the scale at which systems are compared. We illustrate this with a simple graphic analysis.

Assume that, for each system (or data set), the relationship between the number of species and area can be described by a function, and that this function may vary among different systems (for our purposes, the form of these functions need not be specified in detail). Furthermore, assume that these systems differ in some environmental parameter of interest. Although we focus on productivity as the environmental parameter of interest, the principles apply to any continuous factor. Our goals, then, are to compare how species richness changes with productivity, and to determine whether and how this relationship changes as a function of spatial scale (i.e. area sampled). This relationship is the sum of abiotic responses of the species to the environmental factor and resulting changes in biotic relationships.

Three general models may characterize the interrelationships among species richness, area and productivity. In the simplest additive case, assume that the species–area relationships are parallel. Each data set is defined by the same function, but the elevations of the line differ (Fig. 1A). As a result, the relationship between species richness and productivity will also be invariant to spatial scale, with the relationships between species richness and productivity differing only by a constant. A plot of species richness versus productivity will produce a single pattern at all spatial scales (Fig. 1D), and plots representing different scales will produce parallel lines.

An alternative arises when the species–area curves are not parallel, but do not cross within the range of observed values of productivity (Fig. 1B). Such a case might arise if the environmental factor and area have multiplicative rather than additive effects on species richness. When the species–productivity pattern is plotted for areas of different size, it remains qualitatively the same, although the quantitative pattern varies (Fig. 1E). Although we illustrate the problem in terms of differences in slope, any variation in the shape of the species–area function results in a similar effect. Because most theories concerning the relationship between productivity and diversity only make qualitative predictions (Rosenzweig, 1995), tests of these theories are not affected by the interaction of area and productivity. However, if one wishes to test theories that make quantitative predictions, or if one wishes to use the pattern to design management plans, considerations of scale (area) are critical, even when patterns are qualitatively the same.

The most interesting challenge arises when species–area curves intersect (Fig. 1C). In this case, one might find one relationship between species richness and productivity when measured at one scale and the opposite relationship when measured at a different scale (Fig. 1F). Now the scale of measurement is critical, and no single relationship represents a privileged perspective of the pattern.

The difference between the situation portrayed in Fig. 1B and that in Fig. 1C is one of scale of interest, as the former is equivalent to the right-hand portion of the latter. If

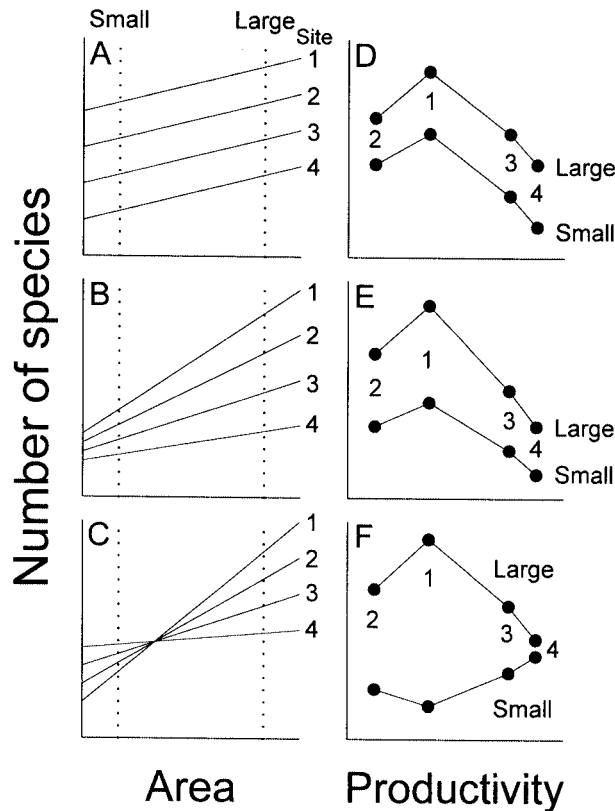


Fig. 1. The effects of invariance of the species–area function on the relationship of productivity and diversity. Parts (A), (B) and (C) illustrate species–area curves for four sites (1–4) that differ in productivity. Scale is not indicated, as any monotonic function would show the same effects. Parts (D), (E) and (F) illustrate the relationship between productivity and number of species across the four sites when sampling at a small and large grain size. In (A) and (D) the relationship is scale-invariant; in (B) and (E) the relationship is rank-invariant; in (C) and (F) the relationship is neither scale- nor rank-invariant. The scales on both axes are arbitrary; the y-intercept does not represent an area of zero.

non-parallel curves exist, then crossing is more likely to occur over greater ecological scales such as across community types. Mittelbach *et al.* (submitted) found that non-monotonic relationships (hump-shaped and U-shaped) are somewhat more common across rather than within community types.

Recognizing such scale-dependencies is important, because it may reveal mechanisms that cause pattern. Thus, it is critical to know whether the curves are scale-invariant (parallel), rank-invariant (non-crossing) or neither. We do not know whether scale invariance is rare or common in nature (but see Lyons and Willig, 1999; Dodson *et al.*, in press). Determining when and where relationships are scale-invariant is a critical and ongoing endeavour (Westoby, 1993; Pickett *et al.*, 1994; Pastor *et al.*, 1996; Rapson *et al.*, 1997).

To demonstrate scale invariance in species–area relationships, we used two sets of data: (1) six old-fields at the Kellogg Biological Station (KBS) LTER site in Michigan, USA

(K. Gross, unpublished data) and (2) 18 tallgrass prairie watersheds at the Konza LTER site (<http://climate.konza.ksu.edu/toc.html>) in Kansas, USA. Each data set consisted of surveys of species of vascular plant. The KBS data were collected in each field using a transect (20×0.5 m) divided into 0.5 m² quadrats. The Konza data were collected in each of 18 watersheds using a set of twenty 10 m² quadrats.

Species–area curves for each field or watershed were derived empirically (Fig. 2). We illustrate this procedure using a single watershed from the Konza data. Species richness per 10 m² was calculated as the mean richness of the 20 quadrats for a watershed. For species richness at 20 m², we first compiled all possible pairwise combinations of quadrats. For each pair, the total number of species was determined. Then, species richness was calculated as the mean number of species for all pairs. For the richness at 30 m², this procedure was repeated using all three-way combinations. This procedure then was repeated and species numbers were determined up to 200 m² (i.e. all 20 quadrats). The resulting species–area curve was not fit to any mathematical function.

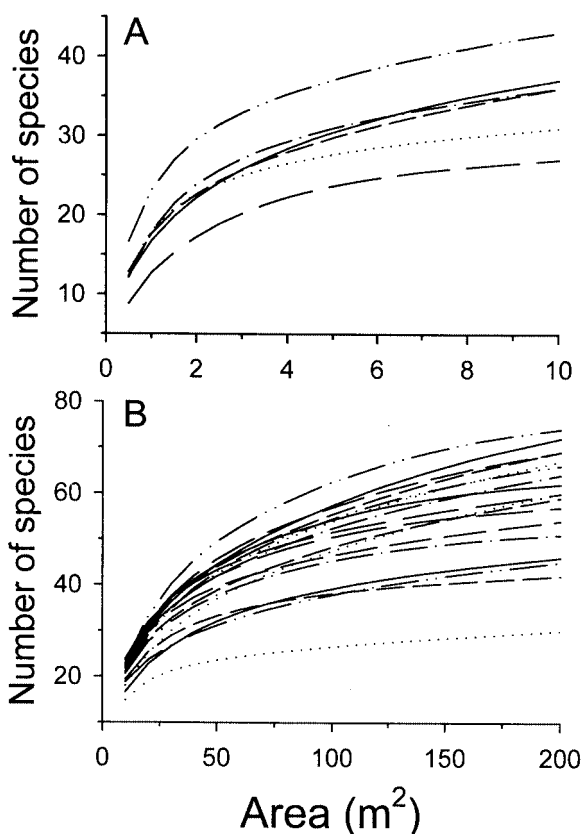


Fig. 2. Estimated species–area curves based on species richnesses calculated from all possible combinations of quadrats. Within each set, the rank-orders of the sample areas do not differ statistically based on the Kendall coefficient of concordance and are rank-invariant within sampling error. (A) Six old-fields in southern Michigan at the KBS LTER site, each consisting of a belt transect (20×0.5 m) divided into 0.5 m² quadrats. (B) Eighteen tallgrass prairie watersheds in Kansas at the Konza LTER site, each consisting of twenty 10 m² quadrats arranged in five transects.

To evaluate rank invariance, we calculated the Kendall coefficient of concordance (W), a measure of multivariate rank correlation, using the mean densities determined at each size (Zar, 1996). We asked whether among watersheds the rank-order of species richness deviated from that expected from a random model. That is, were the rankings of richness at each scale (e.g. 10 m² and 20 m²) more similar to one another than expected by chance. This test is the most direct and most powerful way to examine rank invariance.

Within both KBS and Konza, samples were highly correlated ($W = 0.838$ and $W = 0.934$, respectively). Tests for whether these correlations differ from 1 (see Appendix) failed to reject the null hypotheses (KBS: $F_{19,19} = 1.193$, $P = 0.67$; Konza: $F_{19,19} = 1.071$, $P = 0.79$). A failure to reject the null hypothesis is equivalent to concluding that deviations from a correlation of 1 are the result of sampling error. Our conclusion that any variation was the effect of sampling is bolstered by the pattern of rank-order changes (Fig. 2). Almost all changes in rank order occurred among single, pair and triplet samples for both data sets. Although these switches could indicate changes in processes at fine scales, they are more likely the result of sampling effects because they are almost entirely concentrated at the smallest scales.

More work on small-scale sampling effects is needed to confirm this conjecture. For example, additional sampling could be done using even smaller quadrats. If the region of rank-switching shifted to smaller sizes, sampling effects would be implicated. Also, the density of individuals, especially of rare species, could be determined. Rare species, with only one or a few individuals in a plot, will make a large contribution to sampling error at these scales (Collins and Glenn, 1991).

Thus, at these scales for these two graminoid-dominated systems, the species–area relationship appears to be at least rank-invariant (non-crossing) given empirical sampling error. An alternative test of scale invariance consists of calculating the species–area curve for each sample and comparing the coefficients of those curves. Because the coefficients of such curves would be estimated with error, the power of any such test would be low. However, because many tests of ecological theories concern qualitative predictions, rather than quantitative ones, a test of rank invariance is often sufficient. Rapson *et al.* (1997) also found rank invariance in temperate herbaceous communities, although no formal statistical analysis was done. In contrast, Pastor *et al.* (1996) found evidence of crossing species–area curves for a series of graminoid-dominated wet meadows resulting in a change in the productivity–richness relationship with scale (their fig. 3). Clearly, more empirical work is needed to answer the question of how often species–area curves are scale- or rank-invariant.

THE COMPONENTS OF SCALE

Any discussion of scale effects must rely on definitions. Although we have no desire to introduce more ecological terminology, in interpreting patterns of species richness one must consider four attributes of scale: sample-unit, grain, focus and extent. Two of these attributes (grain and extent) are in common usage. Sample-unit is an obvious extension of current usage. It is the notion of focus that is new.

Sample-unit refers to the spatial and temporal dimensions of the collection unit (e.g. a 1 m² quadrat sampled at the end of the growing season). Grain is the standardized unit to which all data are adjusted via interpolation or extrapolation techniques, if necessary, before analysis. This aspect of scale becomes particularly important in macroecological research when data are obtained from different studies or by different researchers using

sample units of unequal size. For example, eight fields may have measures of species richness derived from 1 m^2 quadrats, whereas one field may have measures of species richness derived from 2 m^2 quadrats. To use data from all nine fields, a standard quadrat size must be selected, which becomes the grain of the study. In theory, the grain could be of any area, but would probably equal the size of the most common sample unit in the entire study (in the earlier example, 1 m^2). A number of algorithms can be used to adjust measures of species richness or productivity in quadrats of 2 m^2 to that in quadrats of 1 m^2 . Some environmental characteristics, such as production, may have a simple allometric relationship to area (intercept of 0, slope of 1); the production of a 2 m^2 area is twice that of a 1 m^2 area. Other characteristics, such as species richness, have a more complex relationship because the richness of a larger area is not in general the simple sum of the richnesses of the constituent smaller areas unless turnover (β diversity) among sampling units is complete. A number of functions (e.g. linear, power, exponential, logistic) could be used to extrapolate from the species richness in a 2 m^2 quadrat to that in a 1 m^2 quadrat.

Focus is the scale at which the grains are aggregated and is equal to or larger than the grain size. For example, when measures of species richness and productivity from each 1 m^2 quadrat are used in the analysis of the relationship between species richness and productivity, the focus is 1 m^2 . In contrast, if data on species richness and productivity are averaged separately for each field, and then the analysis is conducted on those mean values, the focus is a field. Finally, the extent of the study is the geographic area of the samples, the time span of the samples, the biological domain of the samples, or the range of values for the independent variable. In the first two cases the extent is spatially or temporally defined, whereas in the last two cases the extent is defined biologically or ecologically.

Consider a hypothetical example (Figs 3 and 4) in which the species composition and productivity of vascular plants were sampled from ten 1 m^2 quadrats, randomly dispersed

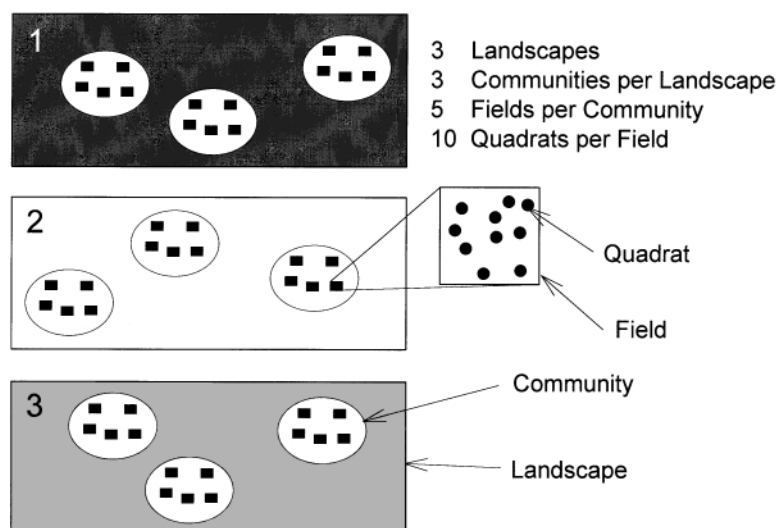


Fig. 3. Diagram of a region illustrating the concepts of sampling-unit, grain, focus and extent. The entire figure represents a region. In this region, there are three landscapes, with three communities in each landscape, five fields in each community and ten quadrats sampled in each field.

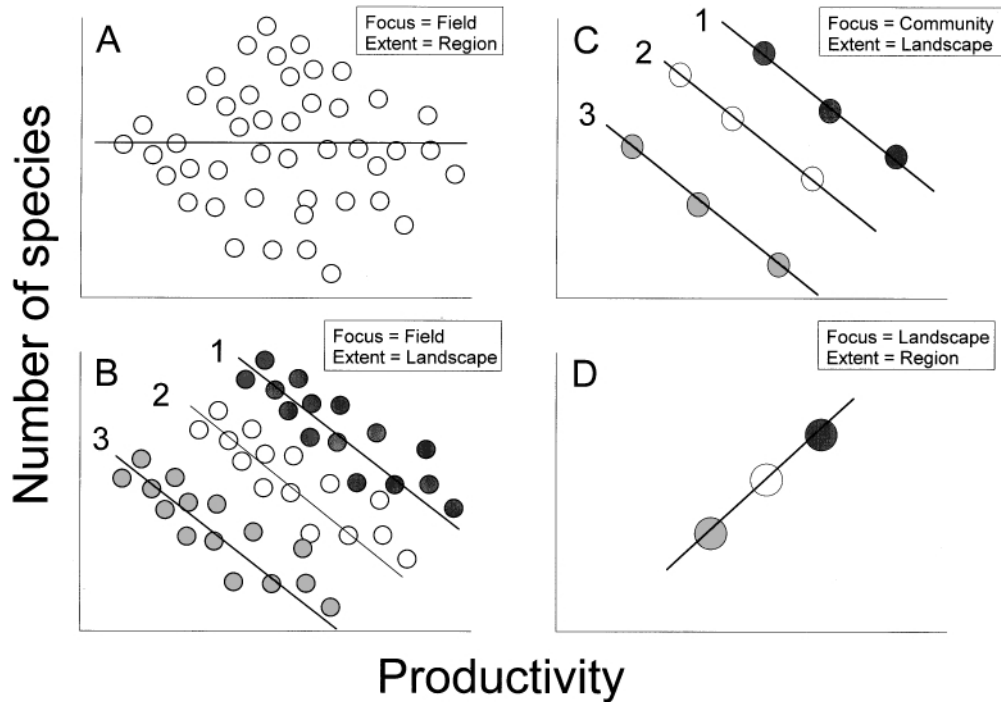


Fig. 4. An illustration of how changing focus and extent alters the relationship between species richness and productivity. In all cases, the sample-unit remains the quadrat and the grain remains the field. Species richness is measured as the total number of species in each field, a grain of 10 m^2 . (A) The focus is the field, the extent is the entire region and the slope is zero. (B) The focus is the field, the extent is the landscape and the slopes are negative. (C) The focus is the community, the extent is the landscape and the slopes are negative. (D) The focus is the landscape, the extent is the entire region and the slope is positive.

in a set of fields. Thus, the sample-unit is 1 m^2 . Five fields were used to characterize each community, and three communities were used to sample each of three landscapes. Within the context of such a hierarchical design, one can assess the relationship between species richness and productivity with respect to four foci (quadrats, fields, communities or landscapes). If all of the data are used, then the extent is the entire region. If quadrats are the focus, then the grain is 1 m^2 . Any relationship studied would be based on species richness per 1 m^2 . In contrast, if the field is the focus of study, then one could characterize each field either by the total number of species in all 10 quadrats or by the average number of species per quadrat. In the former case, the grain is 10 m^2 , and in the latter case, the grain is 1 m^2 . In both cases, the extent remains the same, the entire region. If community is the focus, then the grain could be 1 m^2 (average species richness per 50 quadrats), 10 m^2 (average species richness per three fields) or 50 m^2 (total number of species in all 50 quadrats). Finally, if landscape is the focus of study, then patterns of species richness could be examined at four different grain sizes: 1 m^2 (average species richness per 150 quadrats), 10 m^2 (average species richness per 15 fields), 50 m^2 (average species richness per three communities) or 150 m^2 (total number of species in all 150 quadrats).

Importantly, the relationship between species richness and productivity can differ appreciably, depending on the grain, extent and focus. In our example, analyses set at different combinations of focus and extent result in non-significant, negative linear or positive linear relationships (Fig. 4). Within the statistical literature, this effect is known as Simpson’s paradox (Simpson, 1951). Thus, the existence of a relationship and the form of the relationship can be scale-dependent. Moreover, empirical evidence documents scale-dependence. For example, the relationship between productivity and diversity was examined for vegetation among landscapes across Iberia (Rey Benayas and Scheiner, submitted). The data were analysed both averaging among sites within a landscape (local species richness; grain = site) and summing across sites (total species richness; grain = landscape). In both cases, the focus was the landscape. The patterns differed at the two grains and were due to different processes; for example, spatial heterogeneity affected total species richness but not local species richness. Thus, the distinction between grain and focus is important if we are to identify the scale(s) at which patterns emerge together with the ecological processes that affect them.

Recognizing the potential for scale-dependent patterns helps guide the search for causal processes by providing insight into how processes operate to affect environmental characteristics. Waide *et al.* (1999) demonstrate that the relationship between species richness and productivity is often unimodal when the data span a number of communities (i.e. between-community types). Consider two ways of generating a unimodal pattern when the extent spans a number of local communities (Fig. 5). The between-community pattern might be a simple sum of local-scale patterns (Fig. 5A), suggesting that there is a general functional relationship between diversity and productivity that applies at both local and regional scales. Alternatively, patterns at the local scale might differ from those at the regional scale (Fig. 5B). In this case, a change in focus results in a change in pattern. This disparity would strongly suggest that processes relating species richness to productivity operate differently at different scales. In this case, more than one function must be used to describe the relationship between local diversity and productivity, and the regional pattern is not clearly derived from these local functions. The former case (Fig. 5A), however, would suggest that either the same processes are operating at both scales or that all processes are acting locally. We refer to this latter effect as the *pattern accumulation hypothesis* because the between-community pattern is a simple accumulation of local effects and patterns (see Guo and Berry, 1998).

GRAIN VERSUS FOCUS

We distinguish two attributes of scale, grain and focus, that at first do not seem distinctive. However, only by recognizing these two attributes will we be able to properly infer the scale at which processes are operating. Consider again the earlier example (Fig. 3) and three combinations of grain and focus: (1) individual quadrats as the unit of analysis so that the quadrat is both the grain and the focus; (2) field as the unit of analysis while averaging the number of species per quadrat so that the quadrat is the grain and the field is the focus; and (3) field as the unit of analysis while summing the number of species across quadrats so that the field is both the grain and the focus.

When comparisons are made across fields, the pattern found in the three instances will be identical *if and only if* a single transformation can simultaneously make all species–area curves linear. This is a more general form of the scale invariance described earlier. If this

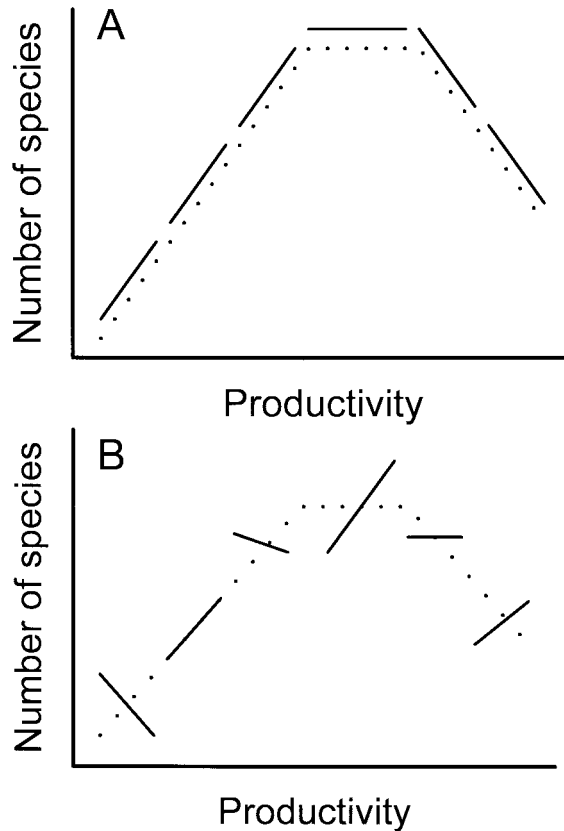


Fig. 5. The relationship between species richness and productivity for a region. Solid-line segments indicate the relationships within various landscapes, whereas the dotted line shows the regional pattern. (A) The regional pattern is a simple sum of the local patterns, suggesting that local-scale processes are responsible for regional-scale patterns, the pattern accumulation hypothesis. (B) The regional-scale pattern differs from the local-scale patterns, suggesting that processes act differently at the two scales.

condition does not hold, the three instances may yield different patterns, depending on details of the data.

But why is it necessary to define a new concept, focus? In the above example, two of the instances have the same grain, but a different focus, while two have the same focus but a different grain. A failure to recognize these distinctions can result in a failure to discriminate between the relative importance of mechanisms that operate at different scales. Moving from pattern to process is one of the grand challenges facing ecology today (Brown, 1999; Lawton, 1999). We currently do not have a simple formula for deducing process from pattern. Yet, the development and testing of theories explaining patterns of species richness is likely to benefit from understanding the link between scale and pattern because different theories have a mechanistic basis at different scales of action.

We emphasize that changing the focus is not the equivalent of investigating the contribution of turnover to total species richness, β diversity. Changing the focus of a study

is changing the inference space to which the question applies. The shape of the species–area relationship is determined by the interaction of local (α) diversity, β diversity and spatial autocorrelations in species distributions. However, there is ambiguity in how α and β diversity are measured. There are no standard scales and methods for their measurement or calculation. We suggest that dealing directly with the species–area relationship, and the parameters of its functional estimate, avoid such problems because scale is always explicit.

Exploring patterns of species diversity in different ecological systems and taxa will generally require combining data collected from many sources. The collection of data will never be the same everywhere. Therefore, it is important to develop a conceptual framework for standardizing or guiding the analysis of data.

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APPENDIX

A test for rank invariance requires testing the null hypothesis that the coefficient of concordance is equal to 1 ($H_0: W_0 = 1$). This coefficient is distributed as a χ^2 -statistic [$\chi^2 = M(n - 1)W$, where M is the number of variables being correlated and n is the number of items within each variable] with d.f. = $n - 1$ (Zar, 1996). An F -statistic is a ratio of two χ^2 -statistics. One can then test the following hypothesis using an F -statistic: $F = \chi^2_0 / \chi^2_i$ (d.f. = $n_0 - 1, n_i - 1$), where χ^2_0 is the χ^2 expected under the null hypothesis and χ^2_i is the observed χ^2 . Substitution gives a test statistic of $F = 1/W$, where W is the observed correlation.