

8 • *Biodiversity Scaling on a Continuous Plane: Geometric Underpinnings of the Nested Species–Area Relationship*

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8.1 Introduction

The species–area relationship (SAR) is considered to be one of the most universal ecological patterns. Indeed, the notion that the number of species recorded within a region should increase as the area of the region increases seems intuitive. No study of diversity patterns in space or time makes sense without accounting for this simple fact (Rosenzweig, 1995). To account for the increase in species richness with area, one needs to know the SAR's properties (e.g. its shape and slope) and the factors that affect them. There is a considerable history of research on this topic (e.g. Arrhenius, 1921; Gleason, 1922; Preston, 1960; MacArthur & Wilson, 1967; May, 1975; Williamson, 1988; Rosenzweig, 1995; He & Legendre, 1996; Hubbell, 2001; Šizling & Storch, 2004; Drakare et al., 2006; Rosindell & Cornell, 2007, 2009; Storch et al., 2007, 2008, 2012; Harte et al., 2009; Lazarina et al., 2013; Storch, 2016; Šizling et al., 2017; see Chapters 3 and 4), but a mechanistic understanding of the underlying causes of SAR properties has emerged only recently. An important component of this understanding is that the drivers of the SAR can be seen as being organized across two hierarchical levels: the geometric and the biological. Each SAR is shaped by biological drivers within the constraints given by geometric rules. Geometry, unlike biology, cannot directly determine actual species richness, but it determines the constraints for the differences in species richness among sites and scales. Geometric rules provide links between the SAR and other macroecological patterns, namely the frequency distribution of species abundances (species abundance distribution, hereafter SAD), species spatial turnover (beta diversity) and, in particular, the spatial distribution patterns of individual species.

8.2 A Typology of SARs

The properties of the SAR and its relationships to other macroecological patterns depend on the way the SAR is constructed (Scheiner, 2003,

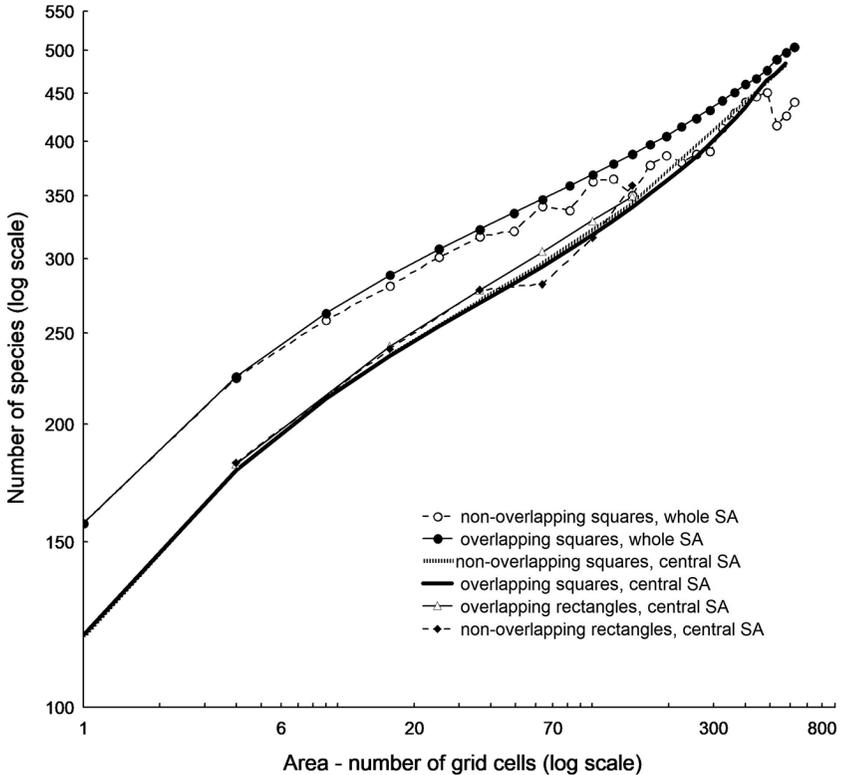


Figure 8.1 An example of the nested SAR constructed using different designs. The nested SAR here is based on the South African Bird Atlas Project (Harrison et al., 1997) in which the area of each grid cell is c. 676 km². The construction depends on 1) the shape of the plots (squares versus rectangles 1 × 4), 2) whether an overlapping or non-overlapping design was used and 3) whether the whole area of South Africa (SA) was sampled (which leads to the situation in which peripheral regions are sampled only by smaller plots) or only a square in the central region (leading to equally intensive sampling for all areas, at the expense of avoiding peripheral areas). These peripheral areas are the most species rich areas in SA and so the nested SARs for the central region lie below those for the whole area. Note that the non-overlapping design for the whole area leads to a fluctuating nested SAR, which can be attributed simply to the incomplete sampling of equal-sized plots that cannot piece together the whole arena. The non-overlapping design leads to a smooth, triphasic nested SAR only in the case of complete sampling, as in the central SA sample area.

2004; Chapter 4). One classical distinction focuses on the differences between island and mainland SARs (Rosenzweig, 1995), but there are actually two mutually independent aspects of this distinction. First, SARs for isolated areas may differ from those for areas that are interconnected by intervening habitat (which facilitates migration), because migration increases the number of species inhabiting smaller areas within which the species could not otherwise have viable populations. However, conceptually more important is the second distinction: whether we examine smaller areas that are nested within larger studied areas or, alternatively, compare mutually disjunct areas differing in size (Tjørve & Turner, 2009). A nested sample design implies strict constraints on species richness at larger spatial scales, as the species richness of larger areas encompasses all the species of the smaller plots within them. In such nested surveys, the species richness of small areas can never be higher than the richness of the larger areas within which they sit. This interdependence of species richness across scales in nested SARs, however, depends on the exact design of the nested sampling (Figure 8.1, Box 8.1). Here, we will focus on nested mainland SARs, as this type of SAR is the most affected by geometric constraints.

Box 8.1 Designing a nested sampling strategy

When constructing nested SARs, the aim is to produce a relationship between area and (mean) species richness that accurately represents the situation in a given region and for a focal taxonomic group. However, ultimately this aim can never be attained due to data limitations and the available techniques for plotting SARs. The major limitations and problems are as follows:

Incomplete sampling. Almost no taxonomic group can be sampled completely within an area; there are always unobserved individuals. Even in apparently complete samples, as is the case of some forest tree plots (Condit et al., 1996), the sample is typically limited by a priori criteria (e.g. minimum diameter at breast height). This leads to lower observed species occupancies and consequently to overestimating nested SAR slopes.

Temporal dynamics. Species populations and communities are not static and the longer we observe a given area, the more species we record. The nested SAR thus interacts with the

species–time relationship (Adler & Lauenroth, 2003; Chapter 19), so that there is a negative interaction between time and area: the longer we observe a community, the lower is the nested SAR slope and vice versa, and smaller areas have steeper species–time relationships (Adler et al., 2005; White, 2007). As in the previous case, this can be attributed to the increase in species occupancy with increasing time.

Finite sampled area. In the case of a nested design, all the sample plots are located within the arena. This has several consequences. Larger plots must either overlap each other or their number has to be limited; both of these effects decrease variation in species richness with sampling area and make our estimation of species richness for larger plots sensitive to the particular placement of the whole arena within the larger region.

Discrete increment of sample sizes. Nested designs are mostly based on finite grids, which means that there is a smallest sample area (one grid cell) and a minimum distance by which a moving window can be shifted. Therefore, it is not possible to estimate mean species richness across all possible plots. If species distributions have a distinctive spatial structure due to some landscape (ir)regularities, this structure may be blurred by using a particular grid. Species occupancies (and thus nested SARs) may thus differ according to the exact position and resolution of the grid.

Shape of sample plots. In the case of a gridded design, squares are the most often used shapes of sample plots. This is obviously not the only possibility. In the case of other designs, the shape of plots may be different and fixed (e.g. individual nature reserves). This can affect the number of sampled species. The role of the shape of a sample plot on plot species richness is poorly explored, although Kunin (1997) showed that elongated samples generally capture more species than square samples of equal area. This is reasonable, given that there is distance decay in similarity in species composition (Nekola & White, 1999) and elongated areas incorporate more distant sites.

Irregular arena. If a nested sampling design is to be used within a region of irregular shape (i.e. one that is not a square or rectangle)

and we still want to use a gridded design, larger sample plots cannot cover the whole area, as they cannot fit into the irregular shape at the periphery of the whole arena (e.g. peninsulas). The areas close to the edge are thus under-represented, which may affect estimated species richness of large areas if peripheral regions differ in species richness from more central regions. It is thus recommended to avoid such incompletely nested designs and restrict the study to arenas where plots of all sizes can be used to sample the whole arena. It is also reasonable to exclude coastal species from sampled islands and/or continents. An alternative approach may be to relax the constraints on sample shape at coarse scales, allowing samples to be fit into the available space or to use the shape of the whole region as the basic shape for all sample areas (Storch et al., 2012).

Since samples of similar area may have different numbers of species, if we plot raw data of species richness against the areas of each sample separately, the relationship may be quite scattered. In most cases, we need a representation of this relationship by a curve for which there is only one value of species richness for a given area. It is thus necessary either to divide the samples into particular size (area) classes and estimate mean species richness across all the plots within each class or to find some mathematical function which best approximates the scattered relationship, typically fit to the data by some form of regression (Chapter 7). If the smoothing function is well chosen, both approaches lead to similar results, as the fitted function approximates the mean values for each area (arithmetic means if we perform a least squares regression in arithmetic space and geometric means if the regression is performed for logarithmically transformed values of species richness). The nested SAR is thereafter a relationship between area and the mean species richness of that area. This is the most obvious way to plot nested SARs and particularly SARs based on grid or transect data. In such a case, it is possible to calculate mean species richness across the windows of given size in the nested design. Constructed in this way, there is a straightforward relationship between the SAR and the spatial distribution patterns of the surveyed species.

8.3 Constraints Imposed by Species Occupancies

Here, we will show how the shape of the nested SAR is determined by the spatial distribution patterns of individual species and demonstrate that the slope of the SAR is driven by patterns of rarity and commonness.

8.3.1 Independence from Interspecific Interactions

Species distributions are spatially complex, with patches and gaps in a species' geographic range across a wide range of scales. One could take a finite set of plots of a given size and calculate the fraction that is occupied by a species, obtaining *relative occupancy* in the case of non-overlapping plots or *probability of occurrence* in the limiting case of an infinite number of mutually overlapping plots. As we cannot have an infinite number of plots in real data, we usually calculate *relative frequency of occurrence*, employing as many overlapping sampling plots as possible. The relative frequency of occurrence is a good estimate of the probability of occurrence and, for the sake of simplicity, most of the literature calls this estimate the probability of occupancy. The relative occupancy is also a good, although slightly worse, approximation of the probability of occurrence. Probability of occurrence tends to increase with the area of the plot. The expected species richness in a random plot of a given area is identical to the sum of the probabilities of occurrence across all the species. Technically,

$$\bar{S}[A] \equiv \sum_{i=1}^{S_{\text{tot}}} p_i[A], \quad (8.1)$$

where A is the area, \bar{S} is the mean species richness, S_{tot} is the total number of species in the whole studied area and p_i is the probability of occupancy attributed to the i -th species (see Coleman, 1981, for relative occupancy, and Šizling et al., 2017 for probability of occurrence). Equation (8.1) implies that species occupancies across the scales considered provide complete information on the nested SAR, which means that no additional information such as specific placement of occupied and empty grid cells for different species can improve the estimate and all relevant biological causes are mediated via the occupancy patterns. This implies that, even though interspecific interactions can affect the co-occurrence patterns of different species (e.g. negative correlations in the case of competition or positive associations in the case of facilitation or other positive interactions), they cannot affect the nested SAR except

insofar as they affect the species occupancies themselves. Such correlations may affect variation around the SAR (i.e. with two positively correlated species, samples would tend to capture either both or neither; whereas for negatively correlated species they would tend to capture either one or the other), but not the mean richness determining the nested, mainland SAR.

8.3.2 Shape of the Relative-Occupancy–Area Relationship

The function which relates probabilities of species occurrence to area can be extracted from occupancy data. The resulting functions are variously referred to as scale–area curves (Kunin, 1998), incidence functions (Ovaskainen & Hanski, 2003), occupancy–area relationships (He & Condit, 2007), range–area relationships (Harte et al., 2005) and P–area relationships (Storch et al., 2008). Although these relationships can be fitted using various mathematical functions (Nachman, 1981; Wright, 1991; Hanski & Gyllenberg, 1997; Leitner & Rosenzweig, 1997; Kunin, 1998; He & Gaston, 2000; for review see He & Condit, 2007), they are generally more or less linearly increasing when plotted on log–log axes (Kunin, 1998), as would be expected for a fractal (self-similar) distribution. However, when examined closely most appear somewhat decelerating across relatively fine scales and accelerating over very coarse scales (Kunin, 1998; He & Gaston, 2000), rather than being precisely linear. At coarser scales, these curves generally reach saturation at a particular area (Šizling & Storch, 2004; He & Condit, 2007). The point at which the curve reaches saturation depends on the relative rarity of the species, that is, on occupancy at the basal scale corresponding to unit grid cells (appendix by Šizling and Storch in Kunin et al., 2018). The probabilities of occurrence and, thus, relative occupancies of rare species reach saturation later than is the case for more common species, depending on the species placement within the total arena.

The finding that a species' occupancy at fine scales (i.e. species rarity) affects the slope of that species' occupancy curve suggests that the overall shape and slope of the nested SAR depends on the proportion of common and rare species in a given assemblage. When the majority of species are widely dispersed, even small sampling areas contain most of the species, as only small gaps in the spatial distributions of species are likely; sampling plots will only rarely fall within these gaps. Further increase in area does not lead to a substantial additional increase in species richness (as most species have already been sampled), which results in

decelerating SARs. In contrast, if rare species predominate, most species will not occur in smaller sampling areas. Species number thus increases quite slowly with increasing area at the beginning, before increasing more rapidly when the sample area approaches the size of the total focal area and the sampling areas have become large enough to sample even the quite rare species. The SAR is consequently upward accelerating in such a case. Natural communities are typically made up of a mixture of common and rare species, and the shape of the SAR at fine scales is more affected by common species, while rare species are responsible for the continuing rise of the curve at large scales (Tjørve et al., 2008). The exact shape, however, depends on the occupancy–area relationships of all species, as the nested SAR is determined by summing these relationships.

8.3.3 Overall Slope of the Nested SAR

One important consequence of the fact that the mean species richness of an area is given by the relative occupancies of all species is that the overall slope of the SAR of a grid, when plotted in log–log space (usually denoted as z), is determined by the mean species occupancy of the unit grid cells in combination with the total number of these unit grid cells (Šizling & Storch, 2004). The rarer the species are, the steeper the SAR will be. This follows from the fact that the overall slope of the log-transformed nested SAR can be estimated from the two endpoints of the relationship: at the upper right end, the total species richness S_{tot} , corresponding to the total focal area (measured in number of unit grid cells) A_{tot} ; and at the lower left the minimum area considered, that of the unit grid cell ($A = 1$) and the mean species richness within the unit grid cell, which is equal to the sum of the species' relative occupancies at this finest scale (see Equation 8.1) (Figure 8.2). The slope of the line defined by these two extreme points in log–log space is then

$$z = \frac{\ln \left(\frac{S_{\text{tot}}}{\sum p_i[1]} \right)}{\ln(A_{\text{tot}})}. \quad (8.2)$$

Since the mean species occupancy at one, $\bar{p}[1]$, equals $\sum_{i=1}^{S_{\text{tot}}} p_i[1]/S_{\text{tot}}$, then $z = -\ln(\bar{p}[1])/\ln(A_{\text{tot}})$. As a consequence, any external or internal factor that affects mean relative species occupancy necessarily also affects the nested SAR slope, so that higher mean relative occupancy leads to a lower nested SAR slope. This is the reason why more productive areas that

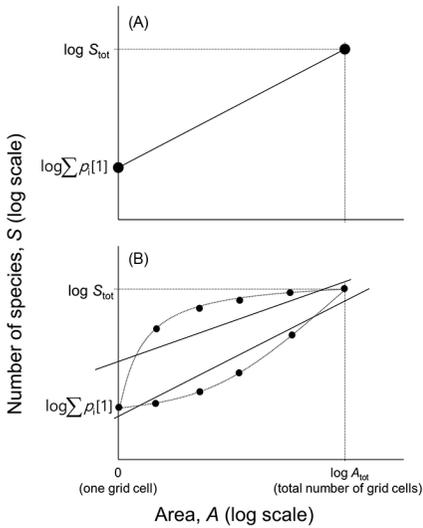


Figure 8.2 The overall slope of the nested SAR and its relationship with mean species relative occupancy for a complete nested design. (A) Assuming that the overall slope of the nested SAR plotted on logarithmic axes is given by the two endpoints of the relationship, the slope is thus determined by mean species occupancy (i.e. the number of occupied cells for each species), total grid size (total number of basic grid cells) and total number of species. (B) If the nested SAR is not linear in a log–log plot, however, the overall slope and the slope estimated using linear least squares regression (solid lines) may deviate from each other, depending on the exact shape of the nested SAR (dotted curved lines) and the differences in the size of the sampling areas (i.e. the distances along the x-axis).

are characterized by higher bird occupancies (Bonn et al., 2004) have lower nested SAR slopes (Storch et al., 2005) and also why higher nested SAR slopes are typical for higher trophic levels which typically have low fine scale occupancies (for a review see Drakare et al., 2006). In line with this finding, lower nested SAR slopes have been reported for plant communities with higher biomass (Chiarucci et al., 2006), later successional stage communities (Lepš & Štursa, 1989; Carey et al., 2006) and for taxa with small body sizes (Azovsky, 2002; Finlay, 2002).

8.4 Constraints Imposed by the Fractal Geometry of Species Ranges

Many mathematical functions have been proposed to model the SAR (Tjørve, 2003, 2009; Dengler, 2009; Chapter 7). The most commonly

used expression is the power law, which is given by $S = cA^z$, where S is the number of species, A is area, c is a constant related to the number of species in a plot of unit area ($A = 1$) and z is the slope of the SAR on a log–log scale (Rosenzweig, 1995). Thus, here z represents the multiplicative increase in species for each multiplicative increase in area (e.g. ‘Darlington’s rule’ that a 10-fold increase in area brings a doubling in species richness is equivalent to a z of $\log(2) \approx 0.3$). The power law was first suggested as a good model for the SAR by Arrhenius (1921; see also Chapter 2) in what was the first formal description of the SAR. It is an advantageous model for several reasons. First, the SAR has been repeatedly reported to be close to linear in log–log space, which means that the power law is indeed an appropriate approximation (Connor & McCoy, 1979; Rosenzweig, 1995; Dengler, 2009). In addition, the power law has been shown to generally provide a better description of the SAR than other common alternatives (e.g. than a logarithmic function of the form $S = k + m \log A$, where k and m are constants, Gleason, 1922), although this may not apply across all spatial scales. Second, and perhaps more importantly, the slope z is a dimensionless number which allows comparison between SARs from different assemblages using a single variable. Third, the z -value of the nested SAR is related to several metrics of species spatial turnover (beta diversity), as we will show in Section 8.9.

That said, it is important to note that there is no reason why the power law should be the universal and invariantly proper description of the SAR. In fact, the power law cannot be a universal description of the SAR across all scales and for all taxa (Storch & Šizling, 2008; Figures 8.3 and 8.4). As mentioned in Section 8.3.1, the nested SAR is determined by summing individual species occupancy–area curves, which in turn are dependent on species’ distribution patterns. The nested SAR can thus potentially have various shapes depending on the proportion of rare and widely dispersed species in an assemblage, and on the occupancy–area relationship of each species. Indeed, insofar as occupancy–area relationships vary in their parameters, there is no reason to expect any simple mathematical function to be the proper and universal description of the nested SAR (Šizling & Storch, 2004), unless the frequency distribution of these parameters was universal across taxa and biomes.

Nonetheless, it does make sense to ask which types of species spatial distributions and which corresponding types of occupancy–area curves lead to particular shapes and slopes of the nested SAR. Is there a particular set of occupancy–area relationships whose sum approaches the power law SAR? It was initially suggested (Harte et al., 1999) that

fractal species spatial distributions (i.e. ones that are self-similar across scales), which produce power law occupancy–area curves, would produce power law SARs. However, this idea was later proved not to be the case (Lennon et al., 2002), as the sum of multiple power laws with different slopes is not itself a power law, but instead tends to accelerate on logarithmic axes. This is a seldom seen pattern in measured nested SARs except at extremely coarse (e.g. continental) scales. However, Šizling and Storch (2004) have shown that the nested SAR can statistically approach the power law if individual species have spatial distributions that are effectively close to fractal and if most species have relatively low occupancies, so that their occupancy–area relationships

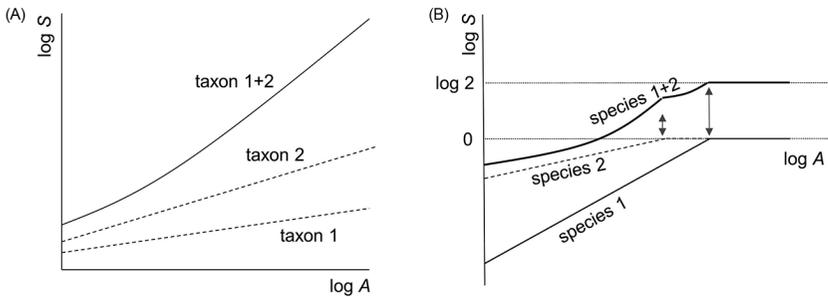


Figure 8.3 The power law approach to the nested SAR cannot be universal across taxa. (A) Let us assume we have two taxa, t_1 and t_2 , which together comprise the higher taxon $t(1+2)$. If the nested SARs for both taxa t_1 and t_2 are power laws with different slopes, the nested SAR for the higher taxon $t(1+2)$ cannot follow a power law, as two power laws form a power law only if both have the same parameters (Lennon et al., 2002; Storch & Šizling, 2008). The power law nested SAR thus cannot be universal across all taxa simultaneously. This can be extended even up to the species level: if the occupancy–area relationships for individual species are power laws with different slopes, the resulting nested SAR is an upward-accelerating curve on a log–log scale (Lennon et al., 2002). (B) A nested SAR approaches a power law (bold line for $s(1+2)$) if the approximate power law occupancy–area curves reveal saturation for some area (arrows) instead of increasing across all scales. This must indeed be the case for any nested SARs measured in a finite area (Šizling & Storch, 2004) (species richness, S , for one species is equivalent to its probability of occurrence within a plot of a given area, which can be estimated using relative occupancy at the respective scale, and S of a single species is thus between zero and one, that is, its logarithm is between zero and minus infinity). In such a case, the upward-accelerating tendency of the nested SAR, driven by summing the power law occupancy–area curves with different exponents, is compensated for by saturation of these curves, which is related to the fact that relative occupancy or probability of species occurrence cannot be higher than 1.

saturate to a value of one at relatively large sampling areas. The tendency for both downward and upward acceleration of the SAR, mentioned above, has a compensatory effect, generating power law like SARs. The fact that occupancy–area relationships are effectively almost linear up to the point of saturation has indeed been commonly reported (Virkkala, 1993; Kunin, 1998; Ulrich & Buszko, 2003; Šizling & Storch, 2004). However, even though self-similar properties of species spatial distributions have been empirically reported, the cause of this pattern was unclear until recently. To explain this observation, Šizling and Storch (2007) and Storch et al. (2008) built a theory of *generalized fractals* to show that patterns which are effectively indistinguishable from fractals can emerge due to any process comprising intraspecific aggregation at multiple spatial scales, for example due to a hierarchy of habitat resolution (so that finely defined habitat patches are nested within habitats defined more broadly). Thus, this theory represents a null model of aggregated species spatial distributions and consequent macroecological patterns.

8.5 Triphasic SARs and Constraints of the Finite-Area Effect

As mentioned above, nested SARs are not properly characterized by the power law across all spatial scales (Hubbell, 2001; Fridley et al., 2005; Storch & Šizling, 2008; Harte et al., 2009; Storch, 2016). First, if we examine sufficiently fine scales, in log–log space the nested SAR typically becomes flatter as the sampling area gets larger, so that the logarithmic function may represent a better approximation than the power law at small scales (Rosenzweig, 1995). This has been attributed by some authors (e.g. Rosenzweig, 1995; Hubbell, 2001) to sampling effects; the number of individuals in such small sample plots is comparatively low and approaches the number of species. As there cannot be more species than individuals, a further decrease in sampling area (and thus the number of individuals) must lead to an increasingly faster decrease of species number. This issue is not trivial and we will deal with it later in the section devoted to the relationship between the SAR and abundance patterns.

A different deviation from the power law has been described as occurring at very large scales (i.e. larger than the extent of whole species ranges), whereby the slope of the logarithmically transformed SAR again increases (Shmida & Wilson, 1985; Storch et al., 2012). This leads

to the notion of a generally triphasic nested SAR (i.e. with downward decelerating, linear and upward accelerating phases in log–log space; Fridley et al., 2005). The upward trajectory of the SAR at very coarse spatial scales is consistent with the behaviour of the individual species occupancy curves discussed above, which bend upwards before reaching saturation. At any scale (resolution) coarse enough that the full range of a species is contained within a single sample area, its occupancy behaves like a single point, resulting in an occupancy curve with a slope that approaches one as area approaches the area of saturation. Allen and White (2003) have shown that the triphasic SAR emerges whenever the distribution of individual species is represented by distinct clumps that are generally smaller than the whole studied area (for instance, if the area comprises whole species ranges; see also McGill & Collins, 2003). A triphasic SAR is also predicted by the neutral model of biodiversity dynamics (Hubbell, 2001; Rosindell & Cornell, 2007, 2009; O'Dwyer & Green, 2010; see Chapter 11), its properties depending on several parameters of neutral dynamics, namely dispersal kernels and speciation rate. Finally, the points that separate the three phases of the triphasic SAR have been shown to depend on the distribution of species range sizes (Storch et al., 2012).

8.6 Constraints Imposed by the Species Abundance Distribution

There have been many attempts to derive the SAR from the species abundance distribution (hereafter SAD; see May, 1975; Williams, 1995; He & Legendre, 2002; Martín & Goldenfeld, 2006; Chapter 4). If individuals were distributed randomly in space, the SAR would effectively be equivalent to a *species accumulation curve* (Gray et al., 2004; Ugland et al., 2005), which is the relationship between mean species richness and the number of individuals drawn from a well-mixed pool. The shape of such a curve entirely depends on the SAD. Such a situation has never been observed, with species spatial distributions generally being more clustered than random (Kunin, 1998; Harte et al., 2005; Storch et al., 2008; McGill, 2010). A SAR derived strictly from random placement would rise relatively quickly to an asymptote once samples were large enough to capture even the rare species and level off thereafter, resulting in a prediction of unrealistically low slopes (and unrealistically high predicted richness) of logarithmically transformed SARs at intermediate to coarser scales.

Further development of these ideas has combined the sampling effect with the spatial aggregation of individuals. Intraspecific aggregation causes larger gaps in species spatial distributions, assuming a given species abundance, which leads to lower mean species richness, as each species occurs in a lower number of quadrats of a given size than would be expected for a random spatial distribution. Evidently, the higher the degree of spatial aggregation of individuals, the higher the overall slope of the nested SAR (z ; He & Legendre, 2002), which resonates with the previous findings described above, if we recognize that high aggregation leads to lower occupancy. According to this approach, therefore, a realistic nested SAR emerges due to the combination of the SAD and the spatial aggregation of individuals (Martín & Goldenfeld, 2006; Tjørve et al., 2008).

The problem with this approach, however, is the assumption that the SAD is given a priori for the whole arena and that SADs of smaller areas can be derived by aggregation (Green & Plotkin, 2007). This assumption would mean that the arena we are studying is ecologically meaningful, where an underlying mechanism produces the abundances of all species within the whole arena. If we choose arenas arbitrarily or such a mechanism does not exist, the SAD would not be general across space and taxa. The reason is that the SAD is not scale invariant and thus SAD form would vary across arenas. Recently, it has been demonstrated that the SAD is not an independent macroecological pattern but itself emerges due to species spatial turnover at multiple scales (Šizling et al., 2009a, b; Kúrka et al., 2010), which is the same pattern that drives the nested SAR. We thus do not need the assumption of a mechanism that centrally controls abundances in large arenas. Generally, there is good reason to assume that the SAD is actually a derived pattern and of limited value as an explanation of the nested SAR.

8.7 Constraints Imposed by the Mean Number of Individuals per Species

Although the nested SAR cannot simply be viewed as being determined by the SAD (in combination with aggregation), species abundances still affect the shape of the nested SAR. Just as we can plot the relationship between mean (expected) species richness and sampling area, we can construct the relationship between the expected number of individuals and the sampling area. Let us call it the ‘individuals–area relationship’ or IAR. Such a relationship must be necessarily linear in a nested design (so

that doubling the area of a sample doubles the mean number of individuals it contains), even in the case of a highly heterogeneous distribution of individuals in space. In a log–log plot (Figure 8.4), the SAR will lie below the IAR, since there can never be more species than individuals. The vertical distance between both curves then equals the logarithm of the mean number of individuals per species (as $\log(I) - \log(S) = \log(I/S)$). The IAR follows a line with slope of one in a log–log plot and thus only the first statistical moment of the SAD, namely mean abundance per species, uniquely determines the shape and slope of the IAR. Such plots make it quite clear that the nested SAR cannot be linear across all scales in log–log space; it thus cannot follow the power law universally. This is because, on one hand, the slope of the nested SAR must be lower than that of the IAR (otherwise doubling the area would lead to doubling the number of species, which can only occur if there were no overlaps in species between sites) and at the same time the nested SAR cannot cross

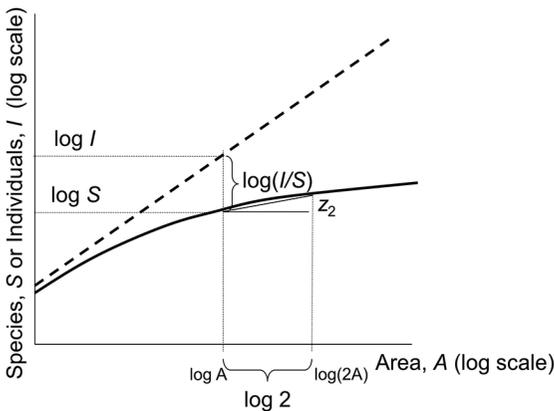


Figure 8.4 The relationship between the nested SAR (bold) and the increase in the number of individuals with area (IAR, dashed). The total number of individuals should increase with area linearly in a completely nested design, which means that it is a straight line with slope equal to one on a log–log scale. Species richness must be lower than the number of individuals for each area, so that the distance between the individuals–area relationship (IAR) and the nested SAR is $\log(I) - \log(S)$, which is equal to $\log(I/S)$, that is, to the logarithm of mean species abundance for a given area. Clearly, if the slope of the nested SAR is (labeled as z_2 , that is, the rate of species richness increase when doubling area) lower than the slope of the SAR for large areas, the same slope cannot be maintained for smaller areas, otherwise the nested SAR would cross the IAR. If the nested SAR is close to the IAR (and thus the mean species abundance is low), its slope must approach the slope of the IAR, that is, it must approach one (modified from Šizling et al., 2011).

the IAR, as the number of species must be lower or equal to the number of individuals (Figure 8.4). This constraint causes the nested SAR to rise steeply (approaching the slope of the IAR, $z = 1$) at very fine scales, where species richness is limited by the number of individuals sampled, but then to decelerate as we move to somewhat larger areas, where the nested SAR and the IAR pull apart from each other. This corresponds to the abovementioned curvature of the nested SAR for small areas, where the number of individuals is too low to encompass a higher number of species. In the limit, when each species is represented by just one individual, species richness increases proportionally to area, that is, the nested SAR slope is 1 and is equivalent to the IAR.

Harte et al. (2009) have argued that the relationship between mean abundance per species and the local slope of the nested SAR (i.e. the derivative of the log–log nested SAR) is a universal function across space and taxa. They have based their approach on Maximum Entropy machinery, which calculates the most likely distribution within particular constraints (see Jaynes, 1957, 1982). Harte et al. (2009) named their approach the ‘Maximum Entropy Theory for Ecology’ (METE). Harte et al. assumed that the total number of species, the total number of individuals and the total energy consumed are conserved at a given area and then derived a one-to-one relationship between the local slope of the SAR and the ratio between the total number of individuals and number of species (i.e. mean species abundance; see Chapter 10 for a discussion of METE and SARs). Although the assumptions may be questionable and the METE approach has several problems (Haegeman & Etienne, 2010) and the discussed relationship cannot apply universally to all taxa (Šizling et al., 2011), it follows from planar geometry of the log–log graph (Figure 8.4) that the local slope of the SAR should indeed be constrained by mean population size of a given area. This can be derived from simple considerations regarding an autocorrelation of the Jaccard index (a proxy for species spatial turnover) across scales (Šizling et al., 2011). The Jaccard index between large adjacent plots is constrained by the Jaccard index for small adjacent subplots. Because the Jaccard index of two adjacent plots scales with z in a one-to-one manner, the constraints upon the Jaccard index determine the constraints for the upper and lower value of z (Šizling et al., 2011). The METE prediction of the relationship runs in the middle between these constraints, but relationships close to the limits are also likely and observed (Šizling et al., 2011). For example, this was found to be the case for an analysis of a British plant dataset,

where the constraints of fractal geometry predicted SAR shape better than METE (Kunin et al., 2018). Note that species abundances are positively related to species occupancies (Gaston et al., 1997) and this finding is thus consistent with the abovementioned relationship between the overall slope of the nested SAR and mean species occupancy (Figure 8.2). This cross-validation of the METE is important for its consistency.

8.8 The Generality of the Nested SAR

Although the claim of generality by the METE has been challenged, there have been several other attempts to find a universal pattern beyond the SAR. Allen and White (2003) showed, using computer-based simulations, that SARs measured on an infinite plane tend to collapse into a universal curve when rescaled by mean species range size and mean richness. Storch et al. (2012) further demonstrated that rescaled SARs extracted from data of five taxa across five continents collapse into a universal curve. Lazarina et al. (2013), however, explored a huge data set on SARs where the arenas were smaller than continents, varying between 0.004 and 27,000 km² and reported considerable deviations from the expected collapse at small and intermediate scales. The deviation from the expected collapse can be attributed to the finite area effect (Šizling et al., 2017): the universal expected collapse fails where species ranges are comparable in size with the arena. This is consistent with the conclusion that the nested SAR is upward accelerating at large scales where ranges are small compared to the whole sampled arena. At small scales, however, where ranges are comparable in size to the sampled arena, SARs vary depending on the frequency distribution of occupancies and areas of gaps within the ranges; both these factors influence the relationship between probability of occurrence and area.

8.9 The Relationship between the Nested SAR and Beta Diversity and Other Macroecological Patterns

The close relationship between measures of species spatial turnover and the slope of the nested SAR in log–log plots (i.e. z in $S = cA^z$) has been repeatedly recognized (Harte & Kinzig, 1997; Arita & Rodríguez, 2002; Koleff et al., 2003; Gaston et al., 2007; Tjørve & Tjørve, 2008) and is in fact quite obvious. If there is no species turnover, an increase in area does

not lead to an increase in the number of species, whereas, if species composition changes rapidly between different plots, any increase in area is followed by a considerable increase in species richness as new areas containing new species are encountered. However, for most formulations developed to date this strictly applies only for measures of species turnover between two equal-area adjacent plots, because in this case the total species richness concerns the contiguous area which is twice the size of each of the original two plots. For instance, Whittaker's (1960) beta diversity index is computed as the ratio between total species richness and the mean species richness of each subplot, $\beta_w = \frac{S_{\text{tot}}}{S_{\text{sample}}}$, and as such it clearly relates to the nested SAR, such that $z = \ln \beta_w / \ln (A_{\text{tot}}/A_{\text{sample}})$, where A_{tot} is the area of the sampled arena and A_{sample} is the area of the sampling plot. Similar mathematical relationships exist for all the beta diversity measures that scale in a one-to-one manner with Whittaker's beta, such as the Jaccard index: the slope z_2 of the logarithmically transformed nested SAR between an area, and an area twice as large can be estimated as $z_2 = \ln \beta_w / \ln 2 = 1 - \ln(1 + J) / \ln 2$, and thus $J = 2^{1 - z_2} - 1$ (Šizling et al., 2017).

Much more problematic is the relationship between the nested SAR and beta diversity for non-adjacent areas. Harte and Kinzig (1997) have derived several macroecological measures in this context, including species spatial turnover and its distance-dependence using the assumption of an exact power law SAR (see also Harte et al., 1999). However, these relationships are only approximate, as they implicitly assume that species turnover between the nonadjacent samples estimates turnover between adjacent samples. These relationships therefore provide realistic predictions only in some cases. So far, the mathematical connections between the nested SAR and the scaling of species turnover (its distance decay; Nekola & White, 1999) are poorly explored (but see Azaele et al., 2008) and represent an exciting area of future research.

The nested SAR is also related to various other macroecological patterns (Storch et al., 2008; McGill, 2010). An obvious example is the regional–local richness relationship (Caley & Schluter, 1997), because regional species richness is simply the number of species in an area larger than that used to calculate local richness, that is, two points in the SAR (Rosenzweig & Ziv, 1999; Bartha & Itzés, 2001). Another pattern which has been related to the SAR is the density–area relationship (e.g. Pautasso & Weisberg, 2008), that is, the observation that population densities are lower if they are measured over larger areas. According to Nee and Cotgreave (2002), this is a simple consequence of the fact that

species richness increases with area, whereas total density (of all species combined) tends to remain constant, so that larger areas are necessarily characterized by lower mean per-species density. As argued above, the increase in richness with area is due to species spatial turnover and thus density–area relationships and community turnover patterns are also mutually dependent.

It is important to note that, in all these cases, it is not always clear what is the primary pattern and what is derived. As we have noted above, all the major macroecological patterns are related to species spatial aggregation at multiple scales (Storch et al., 2008), which can then be considered as the pattern which drives all the other macroecological patterns (McGill, 2010). However, in contrast to the traditional view that

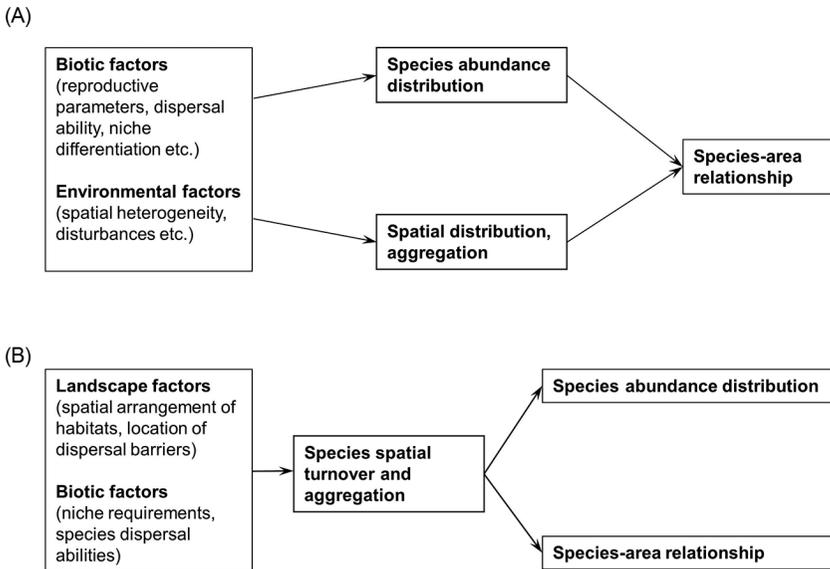


Figure 8.5 The problem of primacy of macroecological patterns which are naturally connected to each other. (A) Many approaches (e.g. He & Legendre, 2002; Martín & Goldenfeld, 2006) assume that the nested SAR can be derived from the SAD in combination with species spatial aggregation, with both of these patterns being determined by different biological factors and processes. (B) However, current findings (Šizling et al., 2009b) indicate that all the patterns are primarily affected by the factors affecting the spatial correlation structure of species distributions, which leads to species spatial turnover and spatial autocorrelation of abundances resulting from aggregation patterns of species distributions. This then leads to many other macroecological patterns, including the SAD.

combines spatial aggregation with the SAD as two independent effects (He & Legendre, 2002), there are good reasons to believe that the truly basic ‘master’ patterns comprise species spatial turnover between neighbouring sites and the spatial autocorrelation of species abundances (Šizling et al., 2009a, b), that is, phenomena that are very familiar to field ecologists (Figure 8.5); the nested SAR and the SAD are then derived from these ‘master’ patterns.

8.10 Conclusions and Perspectives

There is no universal nested SAR that is observed in all situations. However, although empirical nested SARs have various slopes and shapes, these properties are tightly related to patterns in species spatial distributions, such that nested SAR properties can be at least partially predicted on the basis of knowledge of these patterns or the biological factors that affect them. This particularly applies to SARs constructed using a fully nested design, where the species richness of larger areas is constrained by the richness of smaller areas and vice versa. Recent research on the relationships of the nested SAR to other patterns has led to several generalizations.

First, the shape and slope of nested SARs are given exactly by the spatial scaling of species occupancies, that is, they are determined by the occupancy–area relationships of the focal species. Species interactions thus affect the nested SAR only if they affect species occupancies, whereas the exact locations and correlations of species presences are not important for the mean species richness of an area. This also implies that the overall slope of the nested SAR measured on a grid is given by the size of the grid (measured in number of grid cells) and mean species occupancy across those finest-scale cells. Therefore, any biological factors that affect mean species occupancy of the studied taxa necessarily affect the overall nested SAR slope.

Second, there is no a priori reason to expect that the nested SAR follows a simple mathematical function. It is quite practical, however, to approach nested SARs across a range of intermediate scales using the power law, which allows comparison between different nested SARs using two parameters: the overall or local slope of the log-transformed relationship, z , and the intercept c . For this reason, it is useful to plot the nested SAR using log–log plots; nonlinearities in these plots reflect deviations from the power law. When examined across a sufficiently wide range of scales, the nested SAR cannot follow the power law and

there are good reasons to expect generally triphasic SARs. Triphasic SARs are actually produced by several models of biodiversity dynamics. However, realistic nested SARs can be produced by any model that incorporates species aggregation at multiple scales, regardless of whether it is habitat heterogeneity or dispersal limitation (or indeed some other property) which is deemed responsible for the spatial clumping of individuals.

Third, there is a tight relationship between the nested SAR and SADs, species accumulation curves and species spatial turnover. We have argued, however, that attempts to derive the nested SAR using sampling from a distribution of abundances may be misleading, as these distributions are themselves scale dependent and are actually determined by the same pattern as the nested SAR, that is, the clumped spatial distribution of individuals and species spatial turnover. Indeed, species spatial turnover is directly related to the slope of the log–log nested SAR at each particular scale and appears to be the underlying factor driving the pattern. Species spatial turnover increases with the level of spatial aggregation of species and decreases with mean species abundance (and also occupancy, see Section 8.3.1), so that it is natural that these factors are directly related to the nested SAR slope.

Regardless of the progress that has been made in understanding the abovementioned patterns and relationships, several issues remain unresolved. The relationship between the nested SAR and the scaling of species turnover (its distance decay) is still poorly understood, which limits our ability to up–scale regional species richness from scattered local samples (e.g. Ugland et al., 2003; Kunin et al., 2018).

The patterns we have described obtain their universality on the basis of geometric constraints and mathematical logic. However, biological processes, such as the spatial aggregation of conspecifics, are crucial in driving finer and more quantitative features of spatial patterns. Observed nested SARs, as well as their proximate drivers (i.e. the spatial distribution of individual species), therefore emerge due to the interplay between geometry and biology.

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