SYNTHESIS

The theory of the nested species–area relationship: geometric foundations of biodiversity scaling

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Abstract

The relationship between sampled area and the number of species within that area, the species–area relationship (SAR), is a major biodiversity pattern and one of a few law-like regularities in ecology. While the SAR for isolated units (islands or continents) is assumed to result from the dynamics of species colonization, speciation and extinction, the SAR for contiguous areas in which smaller plots are nested within larger sample areas can be attributed to spatial patterns in the distribution of individuals. The nested SAR is typically triphasic in logarithmic space, so that it increases steeply at smaller scales, decelerates at intermediate scales and increases steeply again at continental scales. I will review current theory for this pattern, showing that all three phases of the SAR can be derived from simple geometric considerations. The increase of species richness with area in logarithmic space is generally determined by overall species rarity, so that the rarer the species are on average, the higher is the local slope z. Rarity is scale-dependent: species occupy only a minor proportion of area at broad spatial scales, leading to upward accelerating shape of the SAR at continental scales. Similarly, species are represented by only a few individuals at fine spatial scales, leading to high SAR slope also at small areas. Geometric considerations reveal links of the SAR to other macroecological patterns, namely patterns of β-diversity, the species–abundance distribution, and the relationship between energy availability (or productivity) and species richness. Knowledge of the regularities concerning nested SARs may be used for standardizing unequal areas, upscaling species richness and estimating species loss due to area loss, but all these applications have their limits, which also follow from the geometric considerations.

Introduction

The increase in the number of observed species with increasing area sampled is one of the oldest and most general ecological patterns (Arrhenius 1921; Rosenzweig 1995). Traditionally, it used to be described as a power-law, i.e. a straight line when both area and species richness are expressed in logarithms, but many other functions have been used (Tjørve 2003, 2009; Dengler 2009). The exact shape of the species–area relationship (SAR) is important. If it was universal and/or predictable, we should be able to predict species richness at larger sample areas than those sampled (i.e. upscale species richness; see Harte et al. 2009) or reliably estimate extinction rates based on area loss (Pimm & Askins 1995; He & Hubbell 2011; Keil et al. 2015). A large body of ecological theory aims to describe the shape of the SAR or derive it from a few simple assumptions (Preston 1960; May 1975;

Coleman 1981; He & Legendre 1996; Šizling & Storch 2004; Martin & Goldenfeld 2006; Storch et al. 2008; Harte et al. 2009), with no apparent consensus. I will argue that such a consensus can be reached when we uncover geometric links between the SAR and species distribution patterns.

There are several distinct types of SAR (Scheiner 2003; Dengler 2009), which also differ in terms of the models and approaches that can be utilized to understand their shape. One possible distinction is between the SAR based on naturally isolated regions like islands or continents and the SAR for more or less arbitrarily delimited areas within one contiguous region (Rosenzweig 1995). However, conceptually more important is the difference between the SAR based on mutually independent areas (either islands or pieces of mainland, e.g. nature reserves) and the nested SAR, in which smaller sample areas are nested within large ones. Since the former case comprises independent sets of

species for each area, respective theory cannot rely on any intrinsic relationships between these sets. Any theory must be then based on assumptions concerning the dynamics of biological diversity, namely the processes of extinction and colonization (MacArthur & Wilson 1963, 1967) and/or speciation (Triantis et al. 2015). In contrast, nested SARs are characterized by mutual dependences of large and small sample areas, as larger areas comprise only the species occuring within smaller areas nested within them and *vice versa* — the sets of species within the smaller areas are constrained by the species pool of large ones. This imposes some constraints on the possible shapes of the SARs. Models of nested SARs may consequently utilize the links between spatial diversity patterns and the geometry of the distribution of individual species (Šizling & Storch 2004; Storch et al. 2008). Note that although the nested SARs could in principle also include the island situation (e.g. individual islands nested within an archipelago), they are most commonly studied within contiguous areas, as only these provide a sufficient range of spatial scales.

Here I will review theory concerning the nested SAR and its link to species spatial distributions. By ‚theory‘, I do not mean a particular model but rather a set of models that cover different aspects of the pattern and that are interlinked by understanding their mutual relationships (Marquet et al. 2014). Indeed, I will show that different phases of the nested SAR can be modelled and understood with different approaches, which together combine to provide a quite clear picture of how the pattern emerges.

The phases of the SAR and universality of its shape

The idea that the SAR may have three distinct phases is quite old, although there was some disagreement as to whether the three phases in the logarithmic space follow a ‘flat–steep–flat’ pattern (Lomolino 2000; Crawley & Harral 2001) or the ‘steep–flat–steep’ pattern (Preston 1960; Shmida & Wilson 1985; Fridley et al. 2005). It is only recently that it has been properly empirically demonstrated that the nested SAR follows the ‚steep–flat–steep‘ pattern — a steep increase at the finest scales (Harte et al. 2009), then a slow-down and then again a steep increase at broad, continental scales (Storch et al. 2012). Empirical support for steeper scaling in the lower phase is relatively straightforward. The initial suggestion that the SAR can be universally expressed as a power-law, i.e. a straight line when both species richness and area are logarithmized (Arrhenius 1921), was first challenged by the finding that when plotting the SAR for small areas, the straight line may instead appear in a semilogarithmic plot in which only horizontal (area) axis is logarithmic, suggesting a logarithmic function for the SAR (Gleason 1922). This implies that the SAR is concave (downward decelerating)

at these spatial scales when both the axes are logarithmized. Semilogarithmic expression of the SAR has been used especially for fine-scale vegetation plots (Rosenzweig 1995; Stohlgren et al. 1995), even though it turned out that the logarithmic function provides a poor fit for most observed SARs (Dengler 2009).

The upper phase of the SAR was originally inferred on the basis of the finding that species richness of areas much larger than those sampled in a given study was considerably higher than an extrapolation based on the power-law (Preston 1960; Shmida & Wilson 1985; Fridley et al. 2005). Therefore, for a long time the convex (upward accelerating) shape was not demonstrated using a standard and consistent sampling protocol across a wide range of spatial scales, but instead was based on one data point for the whole region. This could have been a problem, as it makes sense to speak in a rigorous way about the overall SAR shape only for a particular and consistent sampling design (Dengler 2008). The shape of the SAR may vary among different sampling designs (Fig. 1). This impeded the possibility of the construction of the whole triphasic SAR across all scales, as the sources of data were always necessarily different for different spatial scales, ranging from the areas close to the size of individual organisms to whole continents. Therefore, although the idea that the SAR should be upward accelerating at very broad scales was theoretically
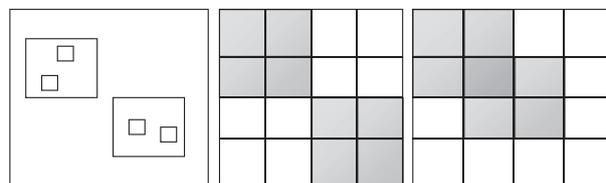
Fig. 1. Different sampling designs used for constructing the nested SAR. Left: Stratified design that selects only a few sample areas (white squares). This can lead to various SAR shapes, depending on the exact locations of sample areas (although, in contrast to non-nested design, it can never lead to decreasing species richness with increasing area). Middle: Gridded data may be overlaid by progressively larger sample areas which, for each scale (determined by the length of respective plot side), do not overlap, but cover the whole region (the grey squares refer to two out of four options for sampling the area of 2 × 2 grid cells). This better represents typical species richness of plots of given area than the previous design. Right: The ‘sliding windows’ design calculates species richness for all possible locations of sample areas for different sizes (here the grey squares represent two out of nine options of sampling the area of 2 × 2 grid cells). This is the best approximation of typical species richness of a given area, even though the sites in the middle of the whole region are sampled more often than those close to the edge (Storch et al. 2008). More problematic is a situation in which the whole study region has an irregular shape (e.g. continents), so that it cannot be fully covered by quadrats (especially large ones). Then one option is to cover it with progressively smaller copies of the shape of the whole region instead of with quadrats (Storch et al. 2012).

derived years ago (Allen & White 2003), it was empirically demonstrated only recently (Storch et al. 2012).

Importantly, when speaking about a general shape of the SAR, we refer to a statistical relationship between area and some typical estimate of species richness within a plot of that area, and not to any possible relationship between area and the number of species. Clearly, if we have many samples for each area that differ in their number of species, we could obtain almost any SAR shape by selection of particular samples, and it is thus not surprising that a SAR based on a limited set of sample areas may substantially deviate from any general shape. Therefore, although the geometric considerations may often apply also for the SARs based on a few selected sample areas as long as they represent typical areas for a given region, by the nested SAR I will hereafter mean only the relationship between area and mean species richness across all sample areas, as it is only in this case that some generalities can emerge. By 'sample areas' I mean contiguous plots of given area – it makes no sense to speak about the SAR if the areas are not contiguous (Dengler 2008, 2009; Dengler & Oldeland 2010; Güler et al. 2016), i.e. in the case of so-called species accumulation curves or collector curves. Such curves are driven by other factors (namely pure sampling effects) and their behaviour is thus different.

Now I will show that each phase of the nested triphasic SAR can be understood based on its own geometric constraints. I will start with broad scales and move to progressively finer scales to demonstrate these constraints.

Large-scale (continental) SAR: the role of range sizes

The nested SAR is tightly related to patterns in the spatial distributions of species (He & Legendre 1996; Šizling & Storch 2004). This is clear from the extremes: if all species were everywhere, the SAR would be a constant function, i.e. its slope would be zero. On the other hand, if every species occupied just one spot (unit area), the number of species would be proportional to area and the slope of the log-log SAR would be one. Real situations are somewhere in-between. Slopes are thus between zero and one, and intuitively it follows that the rarer species are on average, the higher the SAR slope should be. This is the basis of the increase of the local slope of the SAR (its derivative in log-log space at a given area) with increasing sample area at broad spatial scales. As the sample area increases, the proportion of species ranges that are smaller than the sample area also increases, elevating the slope. In other words, when many of the species ranges are relatively small, the slope is high, and this happens only when the sample areas are considerably larger than the majority of species ranges.

This idea was formally developed by Allen & White (2003) using a simplifying assumption of circular ranges,

and later supported by Storch et al. (2012) empirically and using simulations based on randomly located square-shaped contiguous ranges of different sizes. Since the local slope is, according to the theory, determined by range size, Storch et al. (2012) predicted that the SARs for different taxa and different continents should collapse into one universal curve when range size (and also species richness) is standardized, i.e. if area is expressed in units corresponding to mean range size for a given taxon on a given continent (and species richness is expressed as the ratio of measured richness to mean richness for the unit area). Indeed, it turned out that these standardized curves collapsed into an universal relationship, in accord with simulations based on an assumption of random positioning of square ranges which were allowed to overlay the boundary of a given domain. This supports the role of range size in shaping the large-scale phase of the SAR.

The collapse of the upward accelerating SARs at the continental scale was not perfect for smaller areas, i.e. for the left part of the SAR (see also Lazarina et al. 2013). This is expected, as the abovementioned theory and simulations assumed convex ranges with no occupancy gaps. This is a good approximation for large sampling areas, as the gaps within species ranges are generally smaller than the sampling areas, and the ranges thus appear more or less contiguous in this resolution. However, smaller sample areas reveal much more complex structures of species ranges at these scales. Understanding the intermediate phase of the SAR thus requires understanding the relationship between the SAR and spatial structure of species distributions, which goes beyond the simple effect of range sizes.

The SAR at intermediate scales: a power-law?

The SAR has been described as following a power-law function mostly at intermediate spatial scales, corresponding to areas smaller than most species geographic ranges (within individual biomes). There have been several attempts to derive the power-law SAR from the species–abundance distribution (SAD), assuming that the total number of individuals is proportional to area, and smaller areas thus represent just smaller samples of the total number of individuals with correspondingly lower numbers of species (Preston 1960; May 1975; Coleman 1981; Williams 1995; He & Legendre 2002; Martin & Goldenfeld 2006). However, a power-law SAR would emerge in this case only under quite unrealistic SADs. Even more importantly, this pure sampling effect is equivalent to the assumption that all species are distributed randomly in space, which is never the case (Kunin 1998; Storch et al. 2008; McGill 2010). Distributions of individual species are always aggregated (either due to habitat heterogeneity or spatial population dynamics and dispersal limitations), which
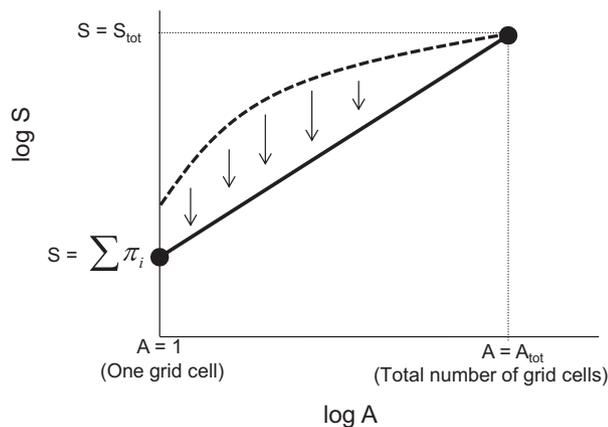
Fig. 2. The effect of aggregation on the SAR slope and the derivation of the SAR slope from mean species occupancy. The SAR determined by pure sampling effect (dashed curve) is equivalent to a SAR of an assemblage characterized by random spatial distribution of individuals of all species, and would be concave in log-log space. Real SARs (full line) are affected also by intraspecific spatial aggregation of individuals, which leads to comparatively lower species richness in smaller sample areas, as the individuals occupy a lower proportion of available sites than in the case of random spatial distributions. Observed SARs are thus located below the sampling-based SAR (except the number of species for the whole study area, which is used as the initial value when modelling the sampling effect), and are more linear in log-log space. The local SAR slope is then more or less constant, and the overall slope can be well estimated from the endpoints of the SAR, i.e. species richness for unit area (e.g. one grid cell) and the whole study region. The slope is then given by (maximum lnS − minimum lnS)/(maximum lnA − minimum lnA), which gives $Z = \frac{\ln\left(\frac{S_{tot}}{\sum \pi_i}\right)}{\ln(A_{tot})}$, where S_{tot} is the total species richness, π_i is the probability of occurrence of species i in a grid cell, and A_{tot} is the total number of grid cells. Since mean species occupancy $\bar{\pi} = \sum_{i=1}^{S_{tot}} \pi_i / S_{tot}$, it follows that $z = -\ln(\bar{\pi}) / \ln(A_{tot})$.

decreases species richness within all sample areas in comparison to random spatial distributions (Fig. 2). Intraspecific aggregation decreases the area occupied by each species, and the species are consequently absent from some sample areas in which they would occur if their distributions were random (they are at the same time more abundant in other sample areas, but this does not affect species richness patterns). Some attempts thus derived the SAR by sampling from the SAD for the whole region, but additionally assuming some level of aggregation. Indeed, McGill & Collins (2003) and McGill (2010) have shown that such a sampling process can explain many observed macroecological patterns.

The problem is that this approach actually requires many assumptions before any predictions can be made. Besides specific assumptions concerning the level of aggregation, it has to be assumed that the SAD for the whole region is something given *a priori* — that it is a

fundamental pattern from which the other patterns are derived. However, Šizling et al. (2009) have shown that the large-scale SAD can instead be derived from the patterns of spatial aggregation (and related patterns of spatial abundance autocorrelation and species spatial turnover) and thus the large-scale SAD may be considered as an epiphenomenon rather than a 'master' pattern. It is therefore reasonable to try to derive the SAR directly from the patterns of species occurrence (species range structure), regardless of the abundance patterns. This approach is justified by the fact that the mean number of species across all plots of a given area is equal to the sum of probabilities of occurrences of individual species in that area (Coleman 1981). The SAR thus can be constructed by superimposition of the functions that relate the probability of occurrence of each species to area (the P_i–area relationship; Šizling & Storch 2004). It has been suggested that these functions are also power-laws, corresponding to self-similar (fractal) species spatial distributions (Harte et al. 1999). Lennon et al. (2002), however, have demonstrated that the superimposition of power-laws with different slopes, corresponding to different properties of each species' distribution, leads to upward-accelerating (convex) SAR in log-log space, instead of a straight line. Nevertheless, this problem disappears in any real (i.e. finite) area, in which the probability of species occurrence for large sample areas is always one, so that even self-similar distributions are characterized by saturated P_i-area functions (Fig. 3), and the resulting SAR may be close to the power-law (Šizling & Storch 2004).

Self-similar species distributions have been reported (Kunin 1998), and thus this explanation of the power-law SAR seems reasonable. On the other hand, the fractal structure of the distribution does not seem to be universal (Hartley et al. 2003; Halley et al. 2004) and its causes are unclear. Fractal species distributions are predicted by some dynamic models (e.g. Scanlon et al. 2007; Kéfi et al. 2011), but these seem too specific (Pueyo et al. 2010). Šizling & Storch (2007) and Storch et al. (2008) have shown that spatial distributions that are almost indistinguishable from self-similar distributions in their effect on the SAR can actually be produced by random spatial aggregations at multiple scales, even if the properties of the distribution are not scale-invariant. For instance, habitat hierarchy in which species-specific microhabitats are nested within more broadly defined habitat types leads to such multi-scale aggregation, which is sufficient to produce a SAR that is reasonably close to the power-law. An approximate power-law thus emerges for a quite broad set of aggregated species distributions. Importantly, it is not clear how accurately SARs at intermediate spatial scales actually follow a power-law. If the SAR is smooth and triphasic in log-log space across all scales, there will always
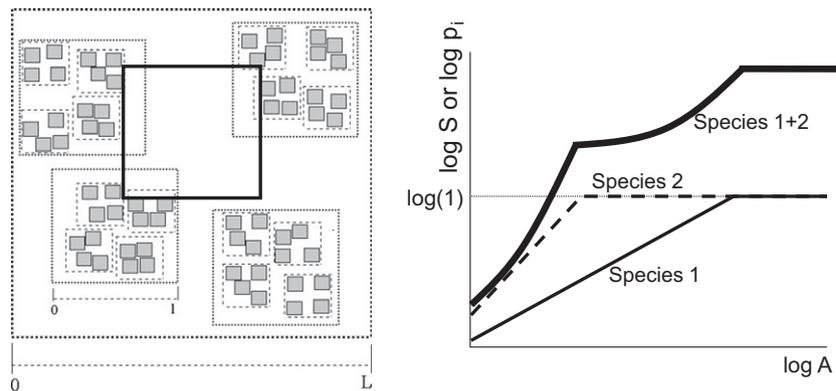
Fig. 3. Relationship between the P_i–area relationships of individual species and the SAR (according to Šizling & Storch 2004) using a two-species example. Here we assume that species spatial distribution can be modelled as a random fractal (left). Such a structure reveals a power-law P_i–area relationship, but only up to area A_{sat}, for which the probability is one. The reason is that probability cannot be higher than one, and there is always an area A_{sat} such that any area larger than A_{sat} (the bold square) always contains the species ($P_i = 1$). The P_i–area relationship is thus saturated (right), and the resulting SAR is not upward-accelerating (as it would be if the P_i–area relationship was just a power-law with a different slope for each species). Instead, the resulting SAR is more complex (bold line), approaching approximate linearity in log-log space when many species are in play (Šizling & Storch 2004).

be some intermediate part which is approximately linear, so that the exact properties of species spatial distributions may not be crucial. In principle, it is possible that the intermediate part of the SAR is more complex, so that the overall SAR is multiphasic instead of just triphasic. However, this is improbable, as there are no strong constraints imposed on its shape at the intermediate scales, and individual species distributions differ in many respects including their levels of occupancy and aggregation. These effects have a tendency to average out, leading most probably to a smooth SAR in logarithmic space, which is approximately linear in its intermediate part.

The nested SAR at intermediate scales has been reported to have a relatively narrow range of slopes, ranging from 0.1 to 0.2, with a modal slope of about 0.15 (Rosenzweig 1995). Using grid maps of species spatial distributions, the approximate slope (exponent) of the power-law SAR can be estimated from the endpoints of the relationship, i.e. by using knowledge of the mean probability of occurrence across all species within unit area (mean species occupancy at the level of one grid cell, $\bar{\pi}$), and the grid size (the total number of grid cells, A_{tot}), according to the equation $z = -\ln(\bar{\pi})/\ln(A_{tot})$ (Šizling & Storch 2004; Fig. 2). Notably, a slope of approximately 0.15 is obtained for a large range of grid sizes when the mean probability of species occurrence in one grid cell is around 0.5 (Storch et al. 2007). This can be considered as the best prior estimate when information is lacking on occupancy probabilities (which must vary between 0 and 1, and 0.5 is just between these values) and also conforms to the observed bimodal – and more or less symmetric – distribution of species occupancies at intermediate scales (Hanski 1982; Storch & Šizling 2002).

The SAR at small scales – the role of the number of individuals

The SAR does not follow a power-law at small spatial scales. The deviation from the straight line in log-log space, however, depends on the sampling design used. In vegetation studies, even parts of individual plants are often counted (i.e. considered as species presence), so that one individual can be recorded in several neighbouring plots. Under this sampling scheme, called 'any part system' (Dengler 2008, 2009), the local SAR slope may eventually reach a value of zero for very small areas (Williamson 2003). This effect disappears when the number of species is counted proportionally to their representation by individuals (e.g. counting one-quarter of species in a unit area if an individual occurs in four neigbouring unit areas) or if we consider only point occurences of individuals (considering only an individual's occupancy centre). Then the local slope of the SAR becomes progressively steeper when approaching small areas (Rosenzweig 1995).

This effect can be easily understood using geometric arguments (Šizling et al. 2011; Fig. 4). In the nested sampling design, mean total number of individuals across all species (I) is proportional to area, and therefore the individuals–area relationship (IAR) is a straight line with a slope of one in log-log space. The SAR must lie below the IAR (as the number of species is necessarily lower than the number of individuals), and has a lower slope (the SAR slope of one would mean that each species occurs only at one spot). Therefore, as the area decreases, the two lines become progressively closer to each other – but since the SAR cannot intersect the IAR for the abovementioned reason, the SAR must be curvilinear in some small areas with
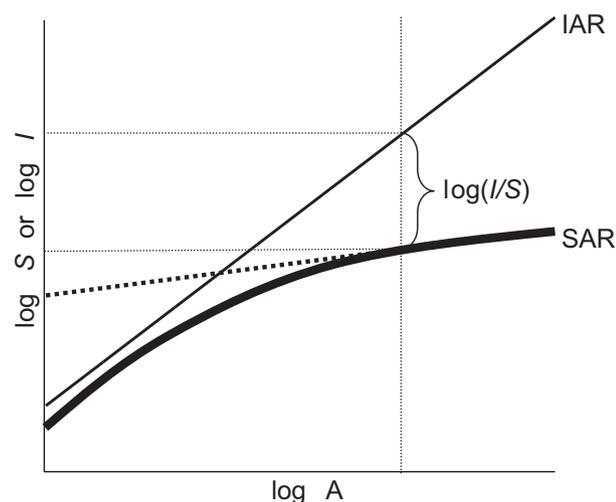
Fig. 4. Geometric reasons for the concave shape of the SAR at small spatial scales. The individuals–area relationship (IAR) is a straight line with a slope of one (this is the geometric necessity that follows from the nested design) and the intercept determined by mean density of individuals. The SAR (bold line) must lie below the IAR (the number of species is always lower than the number of individuals) and must have a lower slope. However, when we move from right to left, i.e. towards smaller areas, the SAR (bold) cannot follow the straight line (dotted line) as it cannot cross the IAR. It thus must be curvilinear, and this curvilinearity is more pronounced when the SAR and IAR are close to each other. The local SAR slope (i.e. its derivative at a given area) thus depends on the distance $\log I - \log S$, which is equal to $\log(I/S)$, i.e. the logarithm of mean population size.

the local slope approaching one. This effect applies universally, regardless of the definition of individuals (i.e. whether genets or ramets are counted) as long as each individual is assigned to only one of several adjacent areas (the grid point system *sensu* Dengler 2008, 2009).

The shape and slope of the SAR is thus constrained at local scales by the limited number of individuals, in a similar way to the constraint imposed by the limited area of species geographic ranges at very large scales. This effect implies that the SAR is steeper the closer it is to the IAR – in other words, the curvature of the SAR should depend on the difference between $\ln I$ and $\ln S$, and since $\ln I - \ln S = \ln(I/S)$, it follows that the SAR local slope should depend on mean species population size (I/S). The lower the number of individuals per species, the higher the slope should be. Such a relationship between mean population size and the local SAR slope was predicted and empirically demonstrated by Harte et al. (2009), albeit using a different method of argumentation coming from maximum entropy machinery (Harte et al. 2008). Later, I will provide more detail about this maximum entropy approach, whose ambition is to provide foundations for major macroecological patterns. Here it is important to

recognize that, qualitatively, the relationship between mean population size and the local SAR slope stems also from simple geometric considerations.

The increase of the local SAR slope at both broad and fine scales has therefore, in some respects, the same cause: at both of these scales, individual species occurrence is limited, either due to the fact that each species is represented by a few individuals (fine scales) or due to the limited extent of its spatial distribution (broad scales). Generally – and almost trivially – the slope of the SAR is determined by the rarity of species at each scale: if the species are spatially restricted relative to the sampled areas, the slope is high, and if they are widespread, the slope is low.

Discussion

The theory reviewed above is based on geometric considerations and very general constraints stemming from mathematical relationships resulting from nested sampling designs. It is thus independent of particular assumptions concerning biological processes responsible for patterns of species distribution and co-existence, and therefore is more general than the majority of theories and models of the nested SAR. Still, it is useful to compare the geometric approach above with other approaches that predict SAR properties. After that, I will discuss implications of the geometric approach to the SAR for patterns in β-diversity, and some links to other macroecological patterns. Finally, I will briefly review a few applications of the SAR.

Other theories of the nested SAR shape

The triphasic nested SAR, or at least some part of it, has been predicted by several prominent theories or models. The most explicit prediction is provided by the neutral theory of biodiversity (NTB; Hubbell 2001; Rosindell & Cornell 2007, 2009). This is not surprising considering that the NTB produces realistic patterns of species abundance and distribution, which represent the basis of the triphasic SAR. Indeed, the lower phase of the SAR is due to the effect of the limited number of individuals in very small areas, as descibed above (Hubbell 2001), while the upper, upward accelerating phase, is driven by spatially restricted species ranges, which are – within the NTB framework – due to dispersal limitation. The inflection point of the SAR is predicted to depend on speciation rate (Rosindell & Cornell 2007), which may be interpreted as resulting from the fact that speciation rate affects mean range size – higher speciation rate leads to higher percentage of young species whose ranges have not yet had time to spread (Storch et al. 2012). The NTB produces intraspecific spatial

aggregation (given by dispersal limitation), which, as I have argued above, produces approximate power-laws at intermediate scales. The triphasic SAR predicted by the NTB thus stems from the same geometric reasons previously explained, although the structure of species distributions follows from the specific dynamics of this individual-based model (see also Grili et al. 2012).

In contrast, the Maximum Entropy Theory of Ecology (METE; Harte et al. 2008) does not assume any particular dynamics, but instead derives the least biased statistical distributions of macroecological variables under particular constraints (namely, constant number of individuals, a given total number of species and total energy consumption of the community at the largest area). It does not predict the upward accelerating phase of the SAR at large scales, as the METE works at within-biome level (Harte et al. 2009). On the other hand, it predicts the first, decelerating phase, and an exact relationship between mean population size and the SAR's local slope. Similar to NTB results, METE's prediction of the SAR is related to the fact that METE predicts aggregated species spatial distributions, and the slope becomes steep due to the limited number of individuals at the finest scales. However, the geometric effects themselves, in contrast to the METE, do not enable exact predictions of a universal shape for the SAR, as envisioned by Harte et al. (2009). This universality predicted by the METE has been questioned by Šizling et al. (2011), who pointed out that it cannot hold simultaneously across differently delimited groups of species, and thus is not taxon-invariant *sensu* Storch & Šizling (2008). It is probable that the universality concerns only the shape of the SAR at very fine scales due to the abovementioned geometric constraints, whereas the SAR shape at intermediate scales may be relatively variable (Šizling et al. 2013; but see Harte et al. 2013). In any case, mean population size remains a crucial predictor of the local slope of the SAR at least at some scales.

There is also a possibility that the overall SAR shape reflects the structure of the landscape, namely variation in the type of habitat heterogeneity when changing scales. Palmer (2007) has suggested that the landscape mosaic is relatively fine-grained at intermediate scales, leading to low SAR slope, while at large scales coarse-grained landscape types determine the upward accelerating phase. It is difficult to evaluate if these effects contribute to the overall SAR shape universally, as they can be quite region-specific, and the type of landscape heterogeneity may vary in a more complex way across scales. In principle, it is possible that some SARs are actually multiphasic due to such effects. However, this is hardly universal, in contrast to the effects of the limited number of individuals at fine scales and limited range sizes at broad scales that drive the major trends in the SAR shape. Habitat heterogeneity certainly affects spatial covariance of species occurrences, as different species may be associated with similar or different habitats. Nevertheless, this would not affect mean species richness for different areas in the case of nested SARs, as long as species occupancies for different areas remain unchanged.

Links between the nested SAR and other (macro)ecological patterns

It has been repeatedly pointed out that the SAR, as a major biodiversity pattern, is fundamentally linked to other macroecological patterns (Harte & Kinzig 1997; Chave et al. 2002; Storch et al. 2008). Most obvious is the link between the SAR and the patterns of species spatial distribution, which directly determine the SAR shape, as shown above. Less straightforward is the abovementioned link to the SAD. Abundance patterns are linked to patterns of species spatial distribution (Brown 1984), but the local slope of the SAR depends only on mean abundance, i.e. the first moment of the SAD (Šizling et al. 2011). On the other hand, the SAD can be derived using knowledge of the spatial structure of populations and communities (Šizling et al. 2009), including the difference in species composition between neighbouring plots. An accurate prediction of the SAD at large areas requires information on how species spatial turnover (or β-diversity) varies over scales as an input, and this information is comprised within the SAR. In this respect, we may turn the argument around and say that, in a sense, the SAD is derived from the SAR. Most precisely formulated, however, both the SAD and the SAR reflect in their own way the spatial structure of communities and populations.

The links between the SAR and β-diversity patterns are relatively obvious (Harte & Kinzig 1997; Arita & Rodríguez 2002; Koleff et al. 2003; Tjørve & Tjørve 2008). Consider two neigbouring plots. If there is information about the total species richness of the two combined plots and the mean number of species in each of these plots, the proportion of species that is shared between plots can be calculated, which is the basis of most β-diversity indices comprising patterns in presence/absence of species. The local slope of the SAR is indeed mathematically related to several β-diversity indices concerning neighbouring plots (Harte & Kinzig 1997; Koleff et al. 2003; Šizling et al. 2011), so that these measures can be derived from each other. The situation is, however, much more complicated for β-diversity of distant plots due to distance decay of community similarity (Nekola & White 1999). Still, the SAR shape and β−diversity are related (and mathematically constrain each other), as they both reflect the level of spatial homogeneity of species distributions and community composition.

The SAR is also potentially linked to other spatial biodiversity patterns. Besides area, species richness increases with energy availability or productivity (Waide et al. 1999; Currie et al. 2004; Šímová et al. 2011, 2013; Storch 2012). There has been an idea that a common mechanism lies behind both the SAR and the SER (species–energy relationship): as area or productivity increases, the total number of individuals of a given taxon also increases, allowing persistence of more species with viable populations (Wright 1983; Hurlbert & Jetz 2010). While this effect may work for independent units like islands or continents, the link between the nested SAR and the SER is more complicated. Area and energy are not mutually exchangeable variables, as the slope of the SAR is usually considerably lower than the slope of the SER, and the effects of area and energy on species richness are not additive, but there is instead often a statistical interaction between them (Storch et al. 2005, 2007; Wang et al. 2009; Hurlbert & Jetz 2010). The sign of the interaction, however, seems to depend on the taxon in focus and on the used measure of energy availability. This is due to the fact that the interaction is mediated by patterns of species occupancy (proportion of occupied area). In more productive areas, species may have higher chances to establish themselves, leading to higher occupancies and thus lower SAR slopes (Storch et al. 2005) – i.e. the interaction is negative. However, if temperature is used as a surrogate for available energy, a positive interaction is often reported (Wang et al. 2009). This is driven by the opposite occupancy patterns – species in warmer environments tend to be rarer (Currie et al. 2004; Quian et al. 2007; Storch 2012), increasing the SAR slope. It is possible that endotherms differ from ectotherms (especially plants) in this respect. In both endotherms and ectotherms, species richness tends to increase towards warmer and more productive regions. However, whereas endotherm population sizes generally increase towards warmer and more productive environments (or remain approximately constant with respect to productivity; see Pautasso & Gaston 2005), plant population sizes decrease as the total number of individuals remains approximately constant due to space limitation (Storch 2012). On the other hand, the SAR has been reported to have a lower slope in plant communities with higher biomass (Chiarucci et al. 2006), resembling in some respects the situation in endotherms. Area and various measures of energy availability thus affect species richness in different ways and their interaction can be quite complex.

Applications of the triphasic SAR

The SAR has been repeatedly used as a tool to (1) compare species richness across areas of different size, (2) upscale species richness to predict diversity at areas larger than the sampled areas, and (3) estimate or predict species loss due to area loss. There are many potential problems with these applications (Smith 2010). For instance, when comparing species richness of areas differing in their size, the effect of area has often been controlled for by fitting a function of the SAR, and then exploring the residuals (e.g. Guilhaumon et al. 2008). However, the results of this procedure obviously depend on the function used and its exact parameters. This function may be based on a theory, but theory is often unable to specify the function including all the parameters without considerable substantial knowledge (see above) and using a simple power-law is risky due to the triphasic SAR shape. Alternatively, the area standardization can be based on a function that empirically fits the data. This raises a risk of losing any signal when some factors affecting species richness co-vary with area. For instance, if larger areas are at the same time the most productive ones, the real effect of productivity would be removed if the empirical SAR was filtered out.

Similarly, the ability to upscale species richness depends on the exact function characterizing the SAR and the assumptions concerning its shape beyond the measured values. Due to abovementioned geometric constraints at the lower and uper ends of the SAR, it is easier to make predictions for very small or very large areas. For instance, knowledge of mean species range size and mean species richness for some intermediate area enables the prediction of diversity at larger areas (Storch et al. 2012). On the other hand, the upscaling is difficult for intermediate areas without detailed knowledge of patterns of species distribution (and we often do not actually need to upscale species richness if we have this knowledge,). The procedure suggested by Harte et al. (2009) is not particularly accurate, as the deviation of empirical local slopes of the SAR from the relationship predicted by METE is so high that the iterative upscaling (for every doubling of area) can produce an error of several orders of magnitude (Šizling et al. 2013; but see McGlinn et al. 2013). Although it is possible to set up the boundaries of species richness at large areas based on richness at small areas and geometric constraints (Šizling et al. 2011), these are very wide and their usefulness is thus limited.

The estimates of current extinction rates face similar problems. These estimates were based almost exclusively on the power-law SARs with particular slopes (Pimm & Askins 1995; Brook et al. 2003; Thomas et al. 2004), assuming that the loss of habitat leads to predictable loss of species richness. This approach was recently criticized (He & Hubbell 2011), but it turned out that the results of He & Hubbell (2011) can be interpreted in terms of the role of the location and shape of the area that is eventually lost (Keil et al. 2015). Moreover, estimates based on the power-law SAR may refer to equilibrium species richness
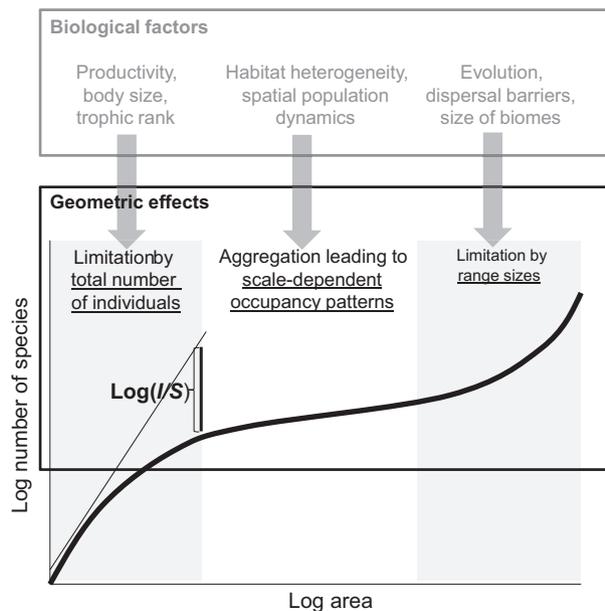
Fig. 5. Schematic of the geometric theory of nested SARs, and the role of biological factors. Each phase of the SAR is constrained by particular geometric effects which thus represent proximate factors affecting SAR shape, namely the limited number of individuals which constrains the local slope of the lower SAR phase, species occupancy patterns at the intermediate phase and limited range sizes at the upper phase. Biological processes influence these proximate factors, thus representing ultimate effects modulating the exact SAR properties. The thin solid line refers to the individuals–area relationship (IAR), the thick line to the SAR. Note that interspecific interactions may affect the nested SAR only via their effect on mean species occupancy, as mean species richness is ultimately determined by the probability of species occupancy of the plots of given area (P_i), and does not depend on the exact location of occupied and unoccupied sites.

within isolated areas (after some part of the area has been lost), and thus to the island SAR (assuming that the remaining areas are contiguous), which is actually relatively well characterized by the power-law (Triantis et al. 2011). Still, the estimates of current extinction rates are very tricky and depend on many assumptions concerning spatial arrangements of lost habitat (Keil et al. 2015), (meta)population dynamics of remaining populations (Rybicki & Hanski 2013), the trajectory towards equilibrium (extinction debt; Wearn et al. 2012; Pe'er et al. 2014) and species persistence in the transformed habitats (Pereira & Daily 2006).

Conclusion

I have reviewed the theory of of the nested triphasic SAR based on geometric constraints concerning the three different phases. Although the whole triphasic SAR can be modelled using one dynamic framework, namely the neutral

theory of biodiversity, I have tried to show that it may be more useful to understand the SAR as a result of several constraints and mathematical relationships operating at different scales (Fig. 5). Generally, the local slope (the derivative) of the SAR depends on species commonness and rarity, i.e. how restricted average species distributions are. Species distributions are relatively restricted at very large (continental) scales, as most species have relatively small ranges in comparison to sampling areas, and thus the local slope of the SAR is high at these continental scales. Individual species occurrence is also limited at very fine scales due to the fact that each species is necessarily represented by a few individuals at these scales, leading to high SAR local slopes for small areas. The resulting SAR is thus triphasic, with the lowest and least constrained slope at intermediate scales, where it depends on patterns of species occurrence and aggregation. At these scales, the SAR can be relatively well represented by a power-law whose slope depends on mean species occupancy (proportion of occupied area), but there is no reason to expect an exact power-law. There is therefore no need to look for an appropriate function best describing the SAR, as its shape predictably varies across scales, and its mathematical expression depends on the relative position of the range of measured areas. The SAR is linked to many other biodiversity patterns, namely the species–abundance distribution and patterns of β-diversity, as all these patterns reflect spatial structuring of communities and populations. Restricted spatial distributions, regardless of their causes, always lead to higher SAR slopes and higher β-diversity. The mathematical properties of the SAR can be used for standardizing species richness measures for plots of different sizes, upscaling species richness, and estimating extinction rates, but these procedures are not very accurate and must be undertaken with caution.

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