CHAPTER FIFTEEN

Scaling species richness and distribution: uniting the species–area and species–energy relationships

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Introduction

Two macroecological patterns of species richness are sufficiently common and occur across such a wide range of taxa and geographic realms that they can be regarded as universal. The first is an increase in the number of species with the area sampled, the species–area relationship (hereafter SAR). The other is the relationship between species richness and the availability of energy that can be turned into biomass – the species–energy relationship (hereafter SER). Both patterns have a long history of exploration (e.g. Arrhenius, 1921; Gleason, 1922; Preston, 1960; Wright, 1983; Williamson, 1988; Currie, 1991; Rosenzweig, 1995; Waide *et al.*, 1999; Gaston, 2000; Hawkins *et al.*, 2003). However, attempts to interpret them within one unifying framework, or at least to relate them to each other, have been surprisingly rare. The most notable exception has been Wright's (1983) attempt to derive both patterns from the assumed relationship between total energy availability (defined as the product of available area and energy input per unit area) and population size. According to this theory, both area and energy positively affect species' population abundances, which decreases probabilities of population extinction, and thus increases the total number of species that can coexist on a site. Then, species richness should increase with increasing area or increasing energy in the same way.

Although this theory can be valid in island situations where the total number of species is determined by the rate of extinctions which are not balanced by immigration events (MacArthur & Wilson, 1967), the situation on the mainland is more complicated. The local occurrence of a species is given not only by the viability of this population itself, but by the broader spatial context (Rosenzweig,

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1995; Gaston & Blackburn, 2000). The shape and slope of the SAR measured on a continuous landscape is thus related to the spatial distribution of species (He & Legendre, 2002), which is affected by total population sizes, habitat heterogeneity (Rosenzweig, 1995), and spatial population or metapopulation dynamics (Hanski & Gyllenberg, 1997; Storch, Šizling & Gaston, 2003a). Consequently, the exact properties of the SER can change with scale (Waide *et al.*, 1999; Mittelbach *et al.*, 2001; Chase & Leibold, 2002), habitat structure (Hurlbert, 2004) and the taxa involved (Allen, Brown & Gillooly, 2002). Moreover, it has been reported that although species richness does increase with environmental productivity, this may often not be the case with population sizes (Currie *et al.*, 2004). This violates the "more individuals hypothesis" of the SER (Gaston, 2000) which states that species richness is higher in more productive areas because they enable persistence of larger populations that are less vulnerable to extinction, in accord with Wright's (1983) proposition.

Given this situation, a simple unified framework for both the SAR and SER seems unlikely to exist. However, the fact that both patterns are inevitably related to patterns in the spatial distributions of species can provide a clue to understanding both of them, as well as their relationship. Every species richness pattern is proximately driven by patterns of occurrence of individual species (both in space and along environmental gradients), and therefore the challenge is to relate species richness patterns to regularities in the spatial distribution of individual species (Storch & Gaston, 2004), and to explore whether similar regularities can be responsible for both the SAR and SER. Our goal is to reveal these connections between the spatial distributions of species and the two biodiversity patterns, and to explore the interrelationships between the SAR and the SER in the light of these connections.

The species–area relationship and spatial species distribution

Traditionally, the increase of species numbers with area within a contiguous mainland has been attributed to three factors (Storch *et al.*, 2003a). The first is a pure sampling effect: larger areas may contain species that are too rare to occur in smaller areas. Second, larger areas contain more habitat types, enabling coexistence of species with different habitat requirements (i.e. habitat heterogeneity is responsible for the increase of species numbers with area). Third, spatial population dynamics leads to an aggregated pattern of species occurrence, such that the probability of finding a species within smaller areas is substantially lower than in larger areas. All these factors apparently contribute to observed SARs, although their relative importance has seldom been tested (but see Storch *et al.*, 2003a). Importantly, although all three inevitably lead to an increase of species richness with area, it is unclear how they contribute to the quantitative properties of the SAR (i.e. its exact slope and shape). These properties seem to be relatively invariant, SARs being well approximated as power laws (but see Tjørve, 2003 for a review of alternative expressions) with relatively predictable slopes (Connor & McCoy, 1979; Rosenzweig, 1995).

A promising way of deriving the slope and shape of the SAR is by studying its proximate cause, the geometry of spatial distribution of individual species. Indeed, all three factors thought to generate an increase of species numbers with area can be seen as ultimate causes of the primary driver of the pattern, the spatial aggregation of species, because of which not all species occur within every possible area (Plotkin *et al.*, 2000; He & Legendre, 2002). Analyzing which types of species spatial distribution lead to which types of observed SARs can be relatively easily done if we define the SAR as the relationship between area and *mean* species number averaged across all plots of a given area. Then the SAR can be obtained by superimposition of functions relating the *probability of occurrence* of an individual of a given species to area. Mean species number (hereafter $\bar{S}$) is exactly equal to the sum of the probabilities of finding every species within a plot of a particular area,

$$\bar{S}_{(A)} \equiv \sum_{i=1}^{S_{\mathrm{tot}}} p_{\mathrm{occ}\ i(A)}, \tag{15.1}$$

where S_{tot} is the total number of species considered and $p_{\mathrm{occ}\,i}$ is the probability of occurrence of species i within plots whose area is A (Coleman, 1981; Williams, 1995; Ney-Nifle & Mangel, 1999; He & Legendre, 2002). It is thus possible to analyze the relationships between A and p_{occ} for different types of species' spatial distributions, and to study how these functions can be assembled to produce the resulting SARs.

The first models of the SAR attempted to derive it on the basis of an assumed random spatial distribution of individuals – this was the case in the widely cited paper of Arrhenius (1921), first describing the SAR as an approximate power law, as well as many of its descendants (e.g. Preston, 1960; Coleman, 1981; Williams, 1995). This assumption can give the power-law SAR, but only for very unrealistic distributions of species abundances (Fig. 15.1; see Williamson & Lawton, 1991). For more realistic species-abundance distributions it predicts a much more rapid increase of species richness for relatively small areas, and relatively quick saturation (Rosenzweig, 1995; Storch *et al.*, 2003a), i.e. rather a logarithmic function than a power law. Moreover, the assumption of a random spatial distribution is plainly unrealistic, except perhaps at very local spatial scales. Therefore, other models were derived which made exactly the opposite assumption of an ideally clumped distribution. That is, they assumed that a better approximation of a species' spatial distribution is a contiguous and spatially restricted geographic range, within which the species occurs everywhere (Maurer, 1999; Ney-Nifle & Mangel, 1999). Again, the model is

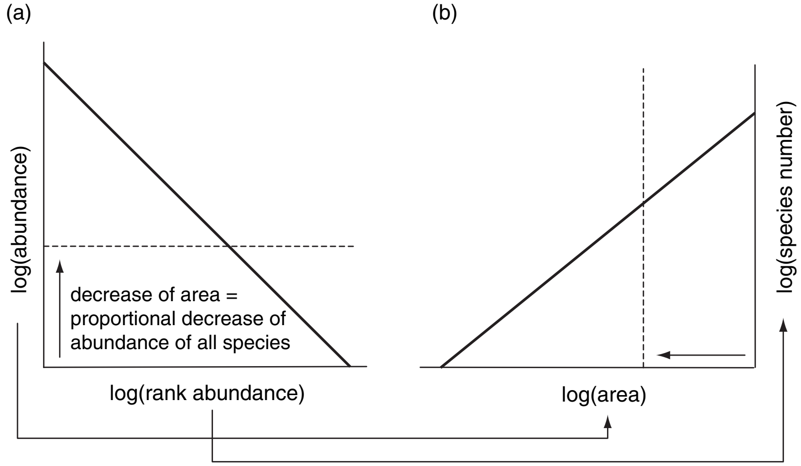

Figure 15.1 Graphical model deriving the power-law SAR from the assumption of the power-law distribution of species abundances and random spatial distribution of individuals. (a) Assume that the rank–abundance curve of an assemblage in the total area is in this case represented by a power law, i.e. log abundance decreases linearly with logarithmized rank. Then the decrease of area to some proportion of the original area is followed by the proportional decrease of abundance of all species, which can be modeled by a shift along the abundance axis (arrow). This leads also to the decrease of number of species, as the abundances of some of them decrease below one. (b) This means that the abundance axis can be understood as equivalent to the area axis, and the rank axis is equivalent to the species number axis. If the slope of the log(rank)–log(abundance) curve is t, then the slope of the SAR $z = 1/t$. Modified from Williamson and Lawton (1991).

unrealistic in its assumption of a homogeneous distribution of individuals within the species' range, and thus fails to predict realistic SARs across all spatial scales, although it seems to be quite appropriate at some scales. Generally, the predicted relationship in this case is a rapid increase of species richness at the beginning, then approximate linearity on a log-log scale (i.e. close to the power law), and then a steep increase again as the spatial scale exceeds the extent of most range sizes (Allen & White, 2003).

Recently, models assuming that species distribution is aggregated on many scales of resolution have been proposed. Harte, Kinzig and Green (1999) were the first fully to acknowledge that the power law indicates scale invariance (or self-similarity), providing a model that explicitly related the power-law SAR to self-similarity at the community level. This model is based on the assumption that if a species is present within an area, the probability of its occurrence within a constant portion of that area remains the same, regardless of the absolute size of the area (see also Harte, this volume). However, using a numerical model, Lennon, Kunin and Hartley (2002) claimed that self-similarity at the level of the distribution of individual species would lead to the power-law SAR

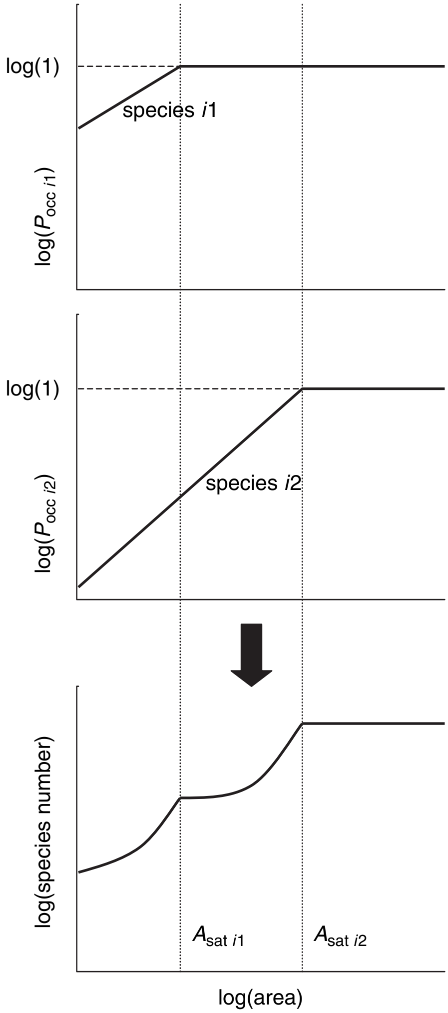

Figure 15.2 Relationship between self-similar species' spatial distribution and the resulting SAR. If species have self-similar spatial distributions, the relationship between their probability of occupancy P_{occ} and area A is approximately a power law (i.e. a line on the log-log scale), but only up to the point A_{sat} where $P_{\mathrm{occ}} = 1$. This point represents the area which contains at least one individual of the species regardless of the position of the plot of this area, and its existence is a necessary consequence of the fact that we measure species distributions within finite areas. If species' distributions were self-similar with different fractal dimensions, the increasing part of their relationships between P_{occ} and area A would have a different slope in log-log space (as is the case here), and the SAR obtained by summing these linear functions using Eq. (15.1) would be upward accelerating on the log-log scale (Lennon *et al.*, 2002). But the fact that these functions are linear and increasing only up to the point A_{sat} (and then they are constant) leads to a more complicated shape, because summing the functions for individual species leads to the upward-accelerating curve only between subsequent A_{sat}. This leads to the SAR which is not exactly linear on a log-log scale, but which mostly does not reveal any apparent upward or downward curvature (according to Šizling & Storch, 2004).

only if all species' spatial distributions had identical fractal dimensions, which seems to be very unrealistic (in fact, it would occur only if all species occupied the same proportions of the total area). Nevertheless, Šizling and Storch (2004) have shown that even if species differ in their fractal dimensions and occupancies, the resulting SAR can be very close to the power law (Fig. 15.2), and that this is indeed the case for central European birds which have a spatial distribution that is indistinguishable from self-similar. That is, if we replace the complex individual species' spatial distributions by exactly self-similar patterns with

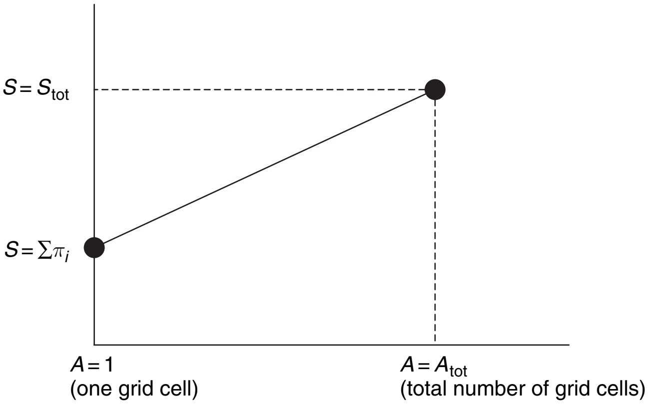

Figure 15.3. Estimating the slope of the SAR from the extremes of the function. As the coordinates of both minimum and maximum of the SAR measured on a grid are given, the slope on the log-log scale can be calculated as $Z = (\ln S_{tot} - \ln \sum \pi_i)/(\ln A_{tot} - n(1))$. This directly gives Eq. (15.2).

fractal dimensions extracted from those observed patterns we get accurate predictions of the shape and slope of the SAR.

This finding has some interesting implications. It suggests that a fractal spatial distribution is a better approximation of a real spatial distribution than is a random distribution or a distribution aggregated on only one spatial level (i.e. a nonstructured geographic range). Although there is no reason that individual species distributions should be fractal in a strict sense (even the abiotic environment is only rarely self-similar, and there is no reason to expect that biological processes should produce preferentially fractal structures; see Palmer, this volume), it seems that this assumption captures quite well the fact that spatial distributions are aggregated on many scales of resolution (Šizling & Storch, this volume). It is even possible that the function relating probability of species occurrence to area is not a bounded power law (which it would be in the case of an approximately self-similar distribution, see Fig. 15.2), but a different function with a similar shape (see He & Condit, and Lennon *et al.*, this volume), that is, an increasing function which becomes saturated for larger areas.

Regardless of the exact nature of species' spatial distributions, the slope of the SAR on a log-log scale for distributions measured on a grid can be calculated on the basis of species' occupancies, i.e. numbers of grid cells where species occur (Šizling & Storch, 2004). The reason is that if the SAR is approximately linear on a log-log scale, we can estimate its slope from its maximum and minimum (Fig. 15.3). The maximum is given by the total area within which we determine species distributions, measured as the total number of grid cells considered, and the total number of species considered ($A = A_{tot}; S = S_{tot}$). The minimum is given by the area of the basic grid cell ($A = 1$) and mean species richness within the basic grid cell, which is equal to the sum of the probabilities of occupancy of one grid cell ($\bar{S} = \sum \pi_i$). The slope of the line defined by these two extreme points in log-log space is then

$$Z = \frac{\ln\left(\frac{S_{\mathrm{tot}}}{\sum \pi_i}\right)}{\ln(A_{\mathrm{tot}})}, \tag{15.2}$$

where π_i is the proportion of grid cells occupied by species *i*. And since mean relative species occupancy $\bar{\pi} = \sum \pi_i / S_{\mathrm{tot}}$, then

$$z = -\ln(\bar{\pi})/\ln(A_{\mathrm{tot}}). \tag{15.3}$$

The implications are straightforward. For a given scale of resolution (i.e. for a given number of basic grid cells) the slope of the SAR on a log-log scale decreases with mean species relative occupancy (i.e. with the mean proportion of sites occupied by each species) and any factor that increases relative occupancies must consequently decrease the slope of the resulting SAR. Interestingly, the most often reported slope of mainland SARs is about 0.15 (0.1–0.2), which corresponds to a mean relative occupancy of about 0.5 for most reasonable grid sizes (Fig. 15.4). The reason why species on average occupy about half of grid cells remains unclear. Nevertheless, there is an explicit relationship between species' occupancy patterns, and the properties of the resulting species–area relationship, which is independent of the exact properties of species distributions and the exact shape of the SAR.

The species–energy relationship and the distribution of species along an energy gradient

The relationship between energy availability (or environmental productivity) and species richness has largely not been considered by studying the distributions of species along the gradient of increasing productivity. This is quite surprising, considering that species distributions are a major proximate driver of any biodiversity pattern. There has probably been an implicit assumption that the increase of species richness with productivity must trivially be accompanied by an increase in species' probability of occurrence. However, there are actually several ways in which species can be distributed along the productivity gradient, and each of them suggests different processes that could be acting (Fig. 15.5).

One extreme is where all species respond to the gradient of energy availability in a similar way, such that they all have a higher probability of occurrence in more productive areas. If this is the case, most species should occupy more localities in more productive areas (there should be fewer gaps in their extent of occurrence) and they should differ only in total range size and/or the range of levels of energy availability under which they occur: whereas common species would occur within the majority of productivity levels (albeit with higher occupancy in more productive areas), rare species would occupy only high productivity levels. The opposite extreme is represented by a "niche division" of species along the productivity gradient: every species occupies only a part of the gradient (sometimes

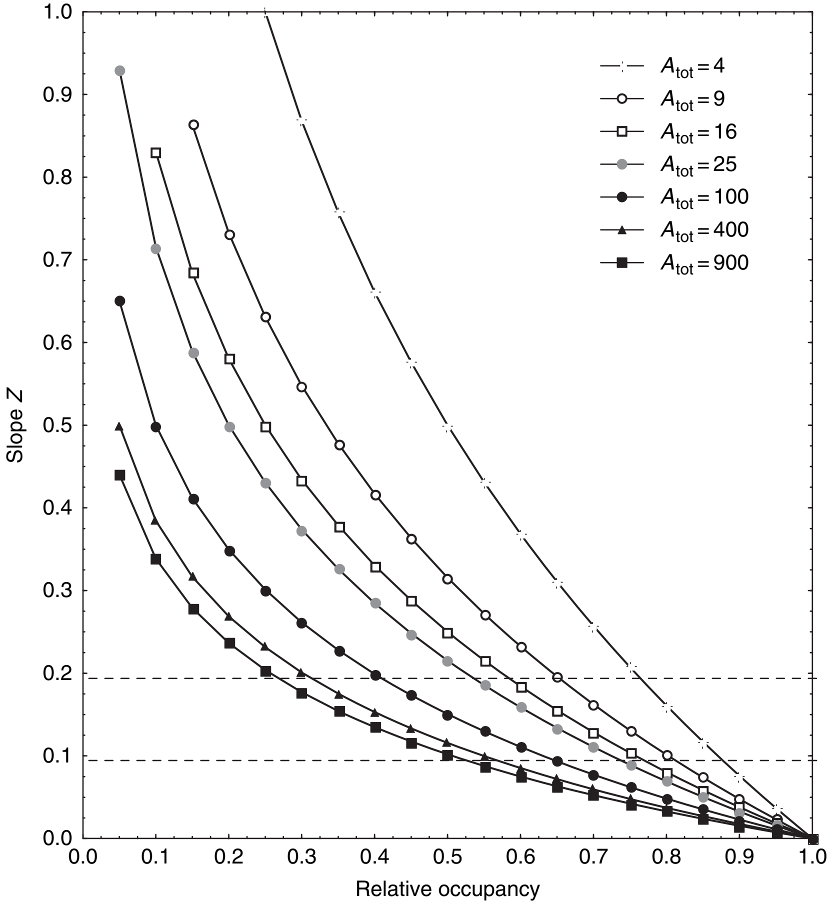

Figure 15.4 Relationship between mean species relative occupancy and the slope of the SAR on a log-log scale. For a reasonable range of A_{tot} (from *c*. 25 to 900 grid cells) the slope falls between 0.1 and 0.2 (dashed lines) when mean relative occupancy is about 0.5 (dotted line). For higher numbers of grid cells relative occupancy should have been lower to fall into that interval; however, grids of more than 30 × 30 cells are rarely considered, and occupancy patterns within such fine grids would probably reflect different processes from those considered here.

narrower, sometimes broader) and the SER is caused simply by the fact that more species are adapted to higher levels of productivity than to lower levels (Kleidon & Mooney, 2000). Whereas the first extreme suggests rather a simple ecological factor (resource abundance etc.) affecting the occurrence of each species independently of every other species, the other extreme indicates that evolutionary forces, such as adaptation, niche division, and species pool evolution, contribute to the increase of species richness with energy availability. Moreover, if every species occupies only a portion of the entire energy gradient (Fig. 15.5a, right), the resulting SER need not necessarily be monotonically increasing. Indeed, the

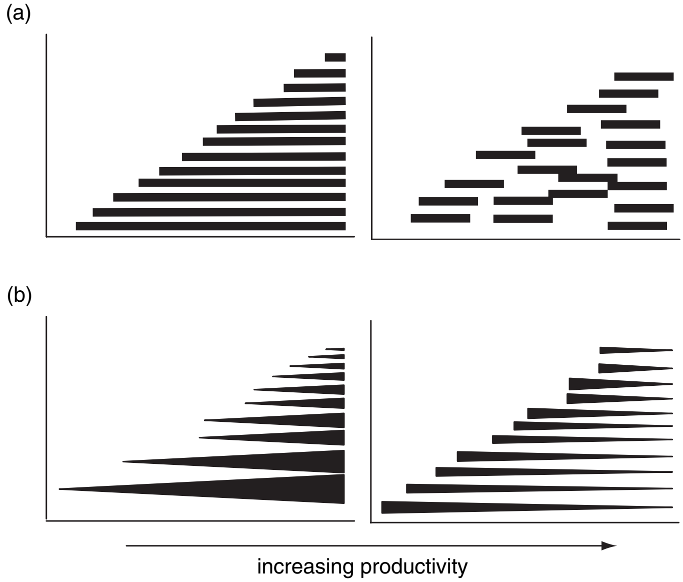

Figure 15.5 Schematic representation of possible ways in which species can be distributed along a productivity gradient; species are represented by individual lines (whose width in row b refers to their relative occupancy). (a) Species distribution can be nested such that all species occupy more productive areas, but only some of them occur also in less productive areas (left), or can restrict their distribution only to some narrow region along the productivity gradient, whose width does not depend on the productivity level (right). (b) All species can occur in a higher proportion of available sites in areas of higher productivity, their occupancy increasing with productivity (left) or their occupancy can decrease as productivity (and species richness) increases (right). Modified from Bonn *et al.* (2004).

reported decrease of species richness within the highest energy levels (Rosenzweig, 1995; Waide *et al.*, 1999; Mittelbach *et al.*, 2001) can be related simply to the fact that species pools for different levels of productivity are different and for high productivity levels are somehow depauperate (e.g. for historical reasons).

It is very probable that both extremes, and anything in between, occur in nature, and that this contributes to the variability of reported SERs. However, it is useful to take a well-resolved data set and explore the real relationship between the SER and the distribution of species along the productivity gradient. For this purpose we took data on bird distributions in South Africa (Harrison *et al.*, 1997), for which species richness increases linearly with productivity (van Rensburg, Chown & Gaston, 2002; Chown *et al.*, 2003), and analyzed the distribution of individual species along the productivity gradient (Bonn, Storch & Gaston, 2004). For all the following considerations we assume that productivity can be measured by the normalized difference vegetation index (NDVI), which has been shown to be closely correlated with net primary productivity (Woodward, Lomas & Lee, 2001; Kerr & Ostrovsky, 2003). The results show that most species conform to the first model, with rare species occurring more frequently within areas of high productivity, whereas common species are those that live in areas of both high and low productivity, as indicated by a substantially lower mean range size of species occuring at high productivity levels (Fig. 15.6c). Moreover, even species occurring in both high and low productivity areas occupy on average more localities in more productive areas, and species turnover between neighboring cells consequently decreases with productivity (Bonn *et al.*, 2004).

The increase of species richness with productivity seems therefore to be related directly to the increase in the probability of occurrence of most species along this gradient. This does not imply, however, that this increase is causally *responsible* for the observed SER. We can ask whether the assumption of increasing probability of species occurrence with productivity is sufficient to explain observed patterns of species richness and distribution – i.e. whether they can be predicted just on the basis of this assumption. To answer this, we have built a simple simulation model of the dynamics of species' geographic ranges across South Africa, based on a few very simple rules (Storch *et al.*, unpublished manuscript). For each species, first, an initial grid cell is chosen for occupancy with a probability that is directly proportional to productivity (i.e. grid cells with double the productivity have double the probability of being selected). Second, each species spreads from this point of origin so that any cell adjacent to any already occupied can be occupied in the next step, but again with a probability proportional to productivity (probability that cell i will be occupied in the next step $P_i = NDVI_i/NDVI_{\mathrm{adj.tot}}$, where $NDVI_{\mathrm{adj.tot}}$ is the sum of NDVI values for all empty cells adjacent to those already occupied). Third, the process stops when the observed number of occupied grid cells is reached (i.e. the observed distribution of species' range sizes is maintained). In the final model (model 4 in Table 15.1), we have also made an additional assumption that the ranges of species are not perfectly contiguous, by adding some random distributional gaps. This was done by enlarging the original range size of each species by a random number of cells between zero and the total number actually occupied, and simulating the dynamics using these new ranges. After each simulation the additional number of occupied cells was randomly set as unoccupied, yielding the observed range size distribution.

The results of this model are quite striking (Fig. 15.6). It predicts accurately the slope of the observed SER (the observed and predicted slopes are statistically indistinguishable), as well as the observed increase of mean species' occupancies along the productivity gradient. Moreover, the mean range size of species occurring within each productivity class (i.e. a set of grid cells sharing approximately the same productivity level) decreases with productivity almost exactly in the same way as observed. Importantly, other models with some of the assumptions relaxed did not produce accurate quantitative predictions (Table 15.1). For example, a model (model 1) that assumed a proportional increase of probability of occurrence with productivity but not spatially

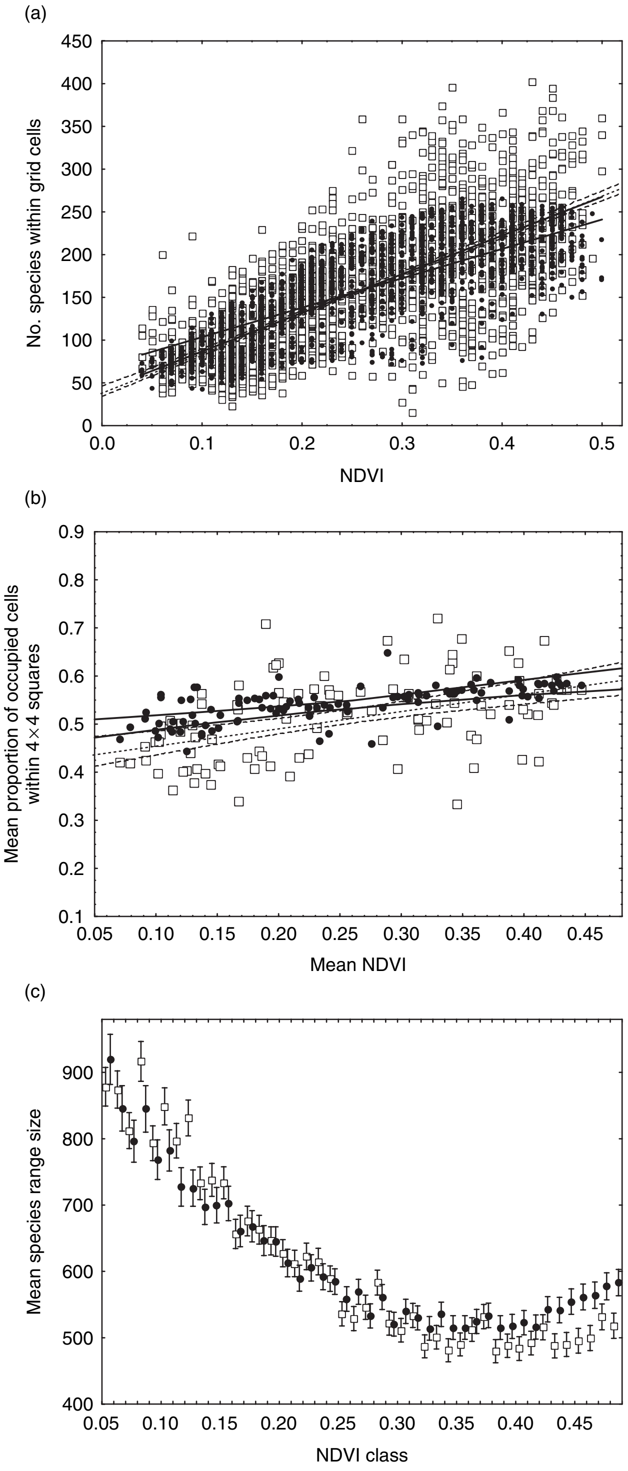

Figure 15.6 Comparison between observed patterns of species richness and distribution along the productivity gradient (white squares) and those predicted by the simulation model (black circles). (a) Relationship between NDVI and species richness for every grid cell; thin dotted line refers to the observed regression line, dashed lines to observed confidence intervals of this line, and bold solid lines refer to nonparametric confidence intervals of the predicted regression lines obtained from 500 simulation runs. Black circles refer to one randomly selected model run. (b) Relationship between mean NDVI and mean relative species occupancy within nonoverlapping squares of 4 × 4 grid cells, the same marking as in the previous case. Mean relative occupancy was calculated as $\frac{1}{S}\sum_{i=1}^{S}\frac{N_{\mathrm{occ}i}}{16}$, where S is the number of species present within the respective 4 × 4 square, and N_{occ} is the number of occupied grid cells for species i. Note that mean relative species occupancy is not equivalent to the probability of occurrence assumed in the model, because whereas occupancy refers to the realized spatial distribution of species within defined spatial units, probability of occurrence always refers to the set of grid cells that can be occupied only in a particular step of range dynamics, i.e. to the potential occupancy of empty available cells at the respective simulation step. (c) Relationship between NDVI and mean range size measured as total number of cells occupied within South Africa, calculated for all species occurring within each NDVI class. The whiskers represent standard errors of means.

Table 15.1 *Comparison of quantitative properties of predicted and observed relationships for four models simulating range dynamics across South Africa, and differing in their assumptions*

Model 1 assumed that species distribute according to productivity without assuming range contiguity, i.e. in each step, one unoccupied cell was set as occupied with $P_i = NDVI_i/NDVI_{\mathrm{tot}}$, where $NDVI_i$ is the value for the particular cell, and $NDVI_{\mathrm{tot}}$ is the sum for all unoccupied cells at a particular step. Model 2 assumed random spreading of contiguous species ranges without accounting for productivity. Model 3 assumed both range contiguity and the proportional increase of probability of occurrence with increasing productivity (see the text). Model 4 added the assumption that species ranges are not perfectly contiguous but contain some (random) amount of gaps. The first two columns give the slope of regression lines for the observation (95% confidence intervals, CIs, of these coefficients in parentheses) and 95% nonparametric CIs of these slopes obtained from 500 model simulations. Underlined are those intervals that overlap with the 95% CIs of observed slopes. Note that these measures of CIs are very conservative, as individual grid cells are not independent of each other due to spatial autocorrelation, and accounting for the autocorrelation would broaden them. The third column gives the proportion of NDVI classes with overlapping standard errors of means of species range sizes for each NDVI class (i.e. total numbers of occupied grid cells across South Africa, calculated for species present in respective NDVI level) between the models and the observation.

	Species-NDVI	Occupancy-NDVI	Range size-NDVI
Observed slope	*457.1* *(435.6–478.7)*	*0.351* *(0.215–0.486)*	
Prediction of model 1	425.4–451.2	0.647–0.677	47.7%
Prediction of model 2	−172.0–32.7	−0.001–0.002	11.4%
Prediction of model 3	485.1–638.6	0.381–0.686	59.1%
Prediction of model 4	343.8–452.1	0.155–0.348	76.7%

contiguous ranges (i.e. species could occupy any unoccupied cells at each step of the simulation, not only those adjacent) predicted the slope of the observed SER quite well, but at the same time predicted too high a slope of the productivity–occupancy relationship, and too rapid a decrease of mean range size with productivity level (because even species with small ranges finally fell into most productivity classes). By contrast, a model (model 2) relaxing the assumption of the relationship between productivity and probability of being occupied (and keeping the range contiguity assumption) did not predict any SER at all.

The fit of model 4 does not mean that it captures all the processes that contribute to the observed SER. In fact, it is quite simplistic, and in some respects unrealistic. For example, all models of stochastic spreading of contiguous ranges necessarily produce the mid-domain effect, i.e. an increase of species richness in the center of a geographic domain due to the inevitable co-occurrence there of species with large ranges (Colwell & Lees, 2000; Jetz & Rahbek, 2001). Our model treated the northern border of South Africa as a hard boundary, not allowing species to spread across it, and consequently artificially strenghtened the mid-domain effect in a north–south direction. Fortunately, this did not affect our results, because the productivity gradient is almost exactly perpendicular to this direction (productivity increases from west to east), and the range dynamics along the productivity gradient (i.e. the spreading of species in the west–east direction) which were responsible for the observed patterns were affected by western and eastern boundaries that are genuinely hard. This has been confirmed by confining all the analyses to the southern part of South Africa, which does not substantially change the results. Nevertheless, the mid-domain effect is an inevitable outcome of simulated dynamics of ranges whose size is comparable to the area of the geographic realm considered, and thus the model would be more appropriate for regions with well-defined hard boundaries.

The findings concerning species distribution along the productivity gradient and the fit of the model have two implications that are relatively general. First, it seems that it is at least sometimes useful to consider the SER as emerging from mutually independent patterns of distribution of individual species along the gradient. Second, the SER has a geographic dimension, which is revealed by the fact that only the model assuming contiguity of species' ranges gave good results. The SER should therefore be viewed from a geographic perspective, as a product of spatial population processes modulated by available energy.

The increase of species' probabilities of occurrence with productivity can have several causes, and does not directly confirm or reject any theory comprising biological mechanisms proposed as explanations of the positive SER (Evans, Warren & Gaston, 2005). One possibility is that it is associated with higher population abundances in more productive areas, and thus is directly linked to the more individuals hypothesis (see above). This is supported by the common observation that abundances and occupancies (and/or range sizes) are positively correlated (Brown, 1984; Gaston, Blackburn & Lawton, 1997; Gaston *et al.*, 2000; He & Gaston, 2000, 2003). However, Bonn *et al.* (2004) have shown for the South African bird data that species' reporting rates – proportions of checklists with presence records for a given species from all checklists submitted for a given grid cell – are lower in more productive areas. And since they are assumed to be correlated with local population abundances, this would not support the simple link between local abundance, occupancy and species richness. The other option would be that small-scale habitat heterogeneity could increase the chance that a species finds a suitable habitat. Heterogeneity may be positively related to productivity (Kerr, Southwood & Cihlar, 2001; Hurlbert, 2004), although the causes and universality of the relationship are unclear, and this option would therefore deserve much more detailed study. Regardless, for now we can rely on the finding that productivity increases the chance of a site to be occupied, irrespective of the biological reason for it.

The species–area–energy relationship

So far, we know that the slope of the SAR on a log-log scale decreases with increasing species' mean relative occupancy, and that species' occupancies increase along a productivity gradient. Therefore, the SAR should have a lower slope in more productive regions, and consequently the SER should be more pronounced for smaller areas. In other words, we should expect a negative interaction between logarithmically transformed area and productivity in their effects on species richness.

We have tested this theory using two of the most comprehensive sets of quadrat-based distributional data, those for bird distributions in South Africa and Britain (Storch, Evans & Gaston, 2005). The results confirmed our expectations: both logarithmically transformed area and available energy were positively related to species richness, with a negative interaction between them even after controlling for spatial autocorrelation (Fig. 15.7). The pattern remained even when using another measure of productivity than NDVI (temperature; following Turner, Lennon & Lawrenson, 1988; Lennon, Greenwood & Turner, 2000), and regardless of whether the productivity measure was logarithmically transformed or not (area and species richness were always logarithmically transformed to obtain comparable slopes of the SAR). Since the slope z of the SAR is one of the possible measures of species turnover (Lennon *et al.*, 2001; Koleff, Gaston & Lennon, 2003), this finding is in accord with that of Bonn *et al.* (2004) that species turnover is lower in more productive areas. In a sense – and quite contrary to common intuition – more productive areas are more homogeneous in terms of geographical differences in the species composition of local assemblages.

Some previous findings seem at odds with the observed patterns. The latitudinal gradient of species richness, for example, has been reported to be more pronounced for large sample areas (Stevens & Willig, 2002; Hillebrand, 2004). If productivity systematically decreased with latitude, as is generally believed (Rosenzweig, 1995), this would challenge our results that the SER is more pronounced in smaller areas. However, latitudinal gradients of species richness are not that simple, and other factors including topography and habitat diversity contribute to them (Rahbek & Graves, 2001; Hawkins & Diniz-Filho, 2004). On some continents, the lower latitudes are even less productive than the higher latitudes: southern parts of North America are considerably drier and less productive than more northern areas (see Hurlbert & Haskell, 2003), and the finding that low latitudes here are associated with SARs of higher slope (Rodríguez & Arita, 2004) is thus in accord with our theory. Indeed, when similar analyses have been performed including humid Central and South America, the pattern predicted by our theory was found, z decreasing toward the tropics (Lyons & Willig, 2002).

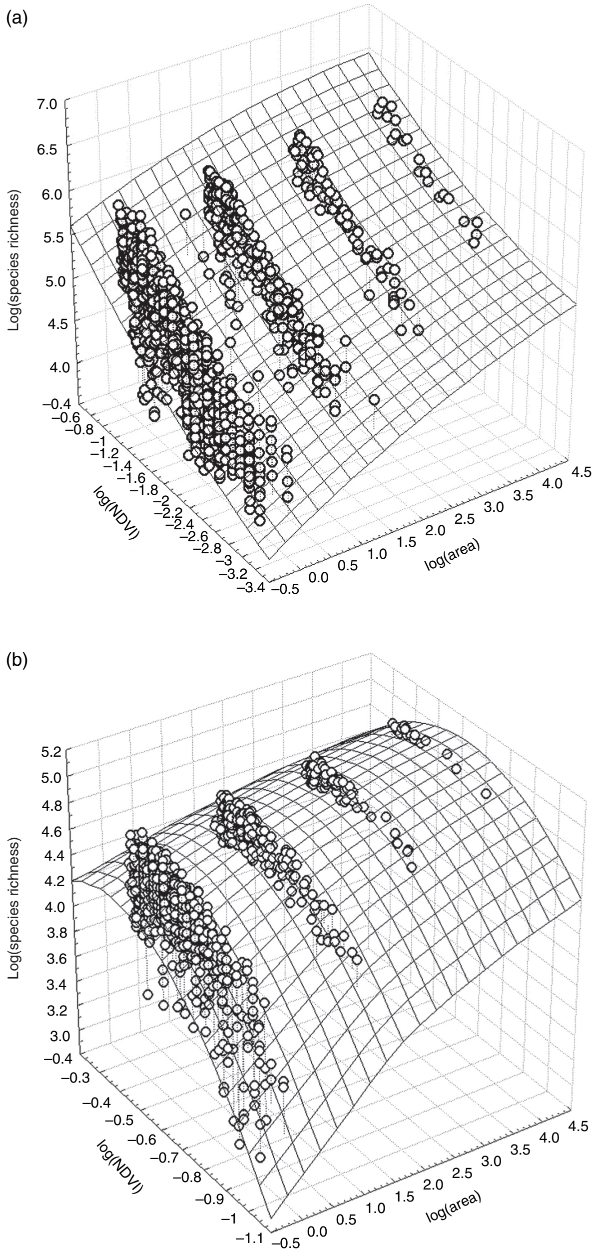

Figure 15.7 Relationship between log(area), log(productivity) and log(species richness) for birds in (a) South Africa and (b) Great Britain. The surface is fitted by spline. Modified from Storch *et al.* (2005).

Our theory thus seems to be rather universal, at least as long as environmental productivity is associated with higher species' occupancies. Note that the theory relating the SAR and SER, as well as their interactions, to patterns of species occupancy (or rather probability of occupancy) treats all species as mutually independent, deriving the patterns without considering any interspecific interactions. This does not mean that interspecific interactions do not exist at the

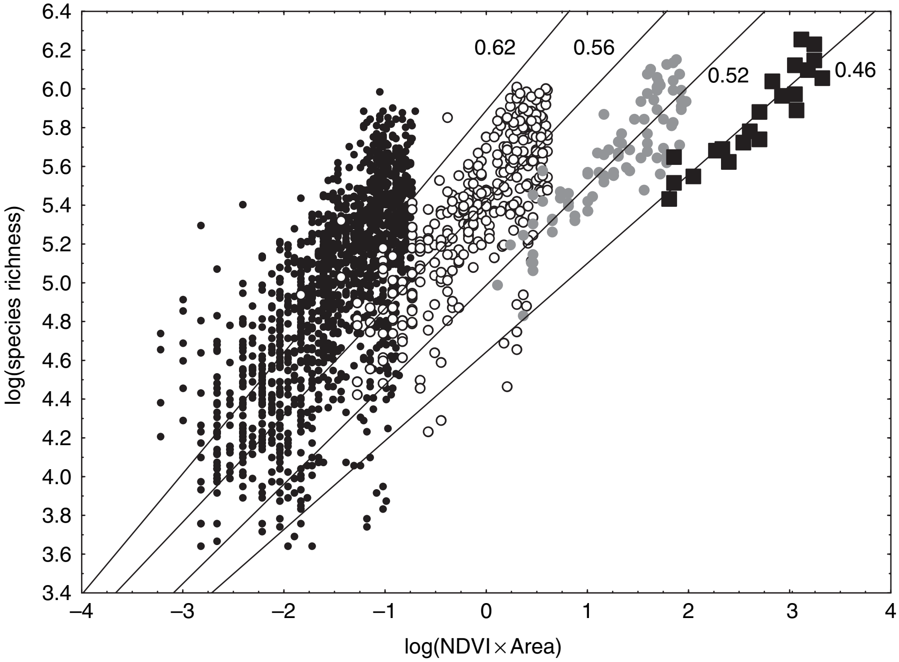

Figure 15.8 Relationship between species richness and the product area × productivity in South Africa, with the relationship for each area marked separately: black dots, basic grid cells; white circles, squares of 2 × 2 (4) grid cells; gray circles, squares of 4 × 4 (16) grid cells; black squares, squares of 16 × 16 (64) grid cells. Regression lines for the relationships (numbers refer to regression coefficients, i.e. slopes of the relationships between species number and productivity in the log-log scale) for different areas indicate that the data points do not fall onto one universal relationship, indicating that the SAR and SER are driven by different factors.

macroecological scale – it is, for example, possible that they determine some species' properties which enter the models as input parameters, especially the distribution of species' range sizes (number of grid cells occupied by each species). However, whenever the species-range-size distribution is given, the species–area–energy relationship with predictable properties emerges, with no necessity to consider species interdependence.

Wright's (1983) notion that the SAR and SER must be closely interrelated has proven to be correct. However, area and available energy do not affect species richness in the same way. According to Wright (1983), the important variable affecting species richness is not area or energy per se, but the product of the two. In that case, the slopes of the SAR and SER on a logarithmic scale should be the same, with no interaction between productivity and area, because an increase in species richness with energy would necessarily be identical for small and large areas. But this is not the case. Moreover, from the plot of species richness against the product of area and energy (Fig. 15.8) we can see that the slope of the SER is considerably higher than the slope of the SAR, and individual samples consequently do not fall onto one general relationship. Note, however, that even if Wright's hypothesis was right, samples of different areas and different productivity levels would fall along one line only if the measure of productivity was exactly proportional to abundance (in the same way as area), which is doubtful in the case of NDVI. Therefore, our data are not too appropriate for a strong test of Wright's original theory, although the negative interaction between NDVI and area indicates that the emergence of the SER and SAR is not as simple as expected by Wright.

Conclusions – what we know and what we don't

We do not provide a definitive mechanistic theory of scaling of species richness with area and available energy. Species richness is apparently affected by many factors acting on different scales of spatial resolution (Whittaker, Willis & Field, 2001; Rahbek, 2005), differing in their biological importance as we move from finer to coarser scales. It is also very probable that the species richness patterns in different taxa emerge due to very different processes; some evidence indicates, for instance, that whereas the richness of endotherms is to a large extent driven by resource abundance constraining the total number of individuals that can be maintained in an area, for ectotherms evolutionary forces such as diversification rate are more important (Allen *et al.*, 2002; Allen, Brown & Gillooly, this volume). This seems quite reasonable, as there is indeed evidence that total abundances and total energy consumption of species assemblages are higher in more productive areas in endotherms (Pautasso & Gaston, 2005), whereas this does not hold for ectotherms (Allen *et al.*, 2002; Currie *et al.*, 2004). However, we show that scaling patterns of species richness are intrinsically linked to patterns of species distribution, regardless of the exact biological mechanisms.

Let us summarize what is actually known, and what is still unknown. First, mainland SARs are proximately driven by aggregated patterns of spatial distribution of individual species, and their slope on a log-log scale can be calculated from mean relative species occupancy (i.e. from knowledge of what portion of the studied area individual species occupy). Moreover, self-similarity is a very good approximation of observed species' spatial aggregation on several scales, but the estimate of the slope of the SAR does not depend on the exact relationship between area and probability of occupancy (which is a power law in the case of self-similarity). We do not know, however, to what extent species' spatial distributions are truly self-similar, and which factors or processes should lead to the apparent self-similarity. One candidate is fractal structure of the environment. Some indications of self-similarity in environmental variables have been found (e.g. Storch, Gaston & Cepák, 2002), although spatial structuring of habitat is quite variable (Palmer, this volume). But habitat is not the only determinant of species distribution, and often cannot sufficiently explain its patterns, spatial population processes being of great importance even in such mobile groups as birds (Storch & Šizling, 2002; Storch *et al.*, 2003a,b). Some random processes of aggregation on several spatial scales (Šizling & Storch, this volume) could provide a clue to understanding scaling of species distributions, but their biological significance (i.e. relationships to habitat structure and population/metapopulation processes) remains unexplored.

Second, we do know that when productivity is positively associated with species richness, it is often associated with a higher probability of occurrence for most species. Moreover, the SER can in some cases be derived directly from the assumption of higher probability of species occurrence in more productive areas, together with some assumptions concerning species' range dynamics. But this pattern may not be universal, and even in the case where it has been documented we do not know its biological causes. The more individuals explanation is probably the simplest and most popular, but the evidence against (Bonn *et al.*, 2004; Currie *et al.*, 2004) indicates that small-scale habitat heterogeneity increasing the chance that a species finds a suitable habitat could be more important (see also Hurlbert, 2004).

Third, we have shown that whenever higher productivity is associated with higher probability of occurrence of individual species, the slope of the SAR on a log-log scale must be lower in more productive areas. But we do not know how universal is the increase of species' occupancies with productivity. If the species richness of ectotherms increases with temperature without an increase in the population densities of individual species (Allen *et al.*, 2002), it is possible that their occupancies also would not increase with productivity – assuming that there is a positive correlation between abundance and occupancy, and between temperature and productivity. Unfortunately, most tests of the relationships between productivity, population sizes, occupancies, and species richness have been performed using data on endothermic animals (particularly birds), for which these data exist at an appropriate resolution (Bonn *et al.*, 2004; Hurlbert, 2004; Pautasso & Gaston, 2005; Storch *et al.*, 2005; but see Kaspari, Zuan & Alonso, 2003 as an exception from this trend).

Finally, we know that scaling of species richness with energy and area can be understood in terms of patterns occurring at the level of individual species, and can be modeled assuming total species independence and no interspecific interactions. This is quite surprising, because most models and theories concerning the SER have assumed that energy availability limits total abundances or biomasses, and that this constraint on the total numbers of species that can coexist at a site is the driving force of species richness differences. But it may not be true if the increase of species richness with productivity is mediated by habitat heterogeneity (see Hurlbert, 2004). However, we do not know to what extent species independence is real, and to what extent it is just a useful property of the models which capture the relationship between several different patterns – which themselves can be affected by interspecific interactions and external constraints limiting the number of individuals and/or species within an area (i.e. any sort of "biotic saturation"). The models we have presented assume that the distribution of species' range sizes is given, and this distribution may in fact reflect the mentioned constraints. Similarly, the increase of species' occupancies with productivity may or may not be related to limits which energy places on species abundance and occurrence. But the lesson is: so far no macroecological species richness pattern itself provides evidence for interspecific interactions or biotic saturation as a major driving force behind it. These effects can be important, but macroecological patterns themselves are not sufficient – as far as we know – for their demonstration.

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