IDEA AND PERSPECTIVE

The quest for a null model for macroecological patterns: geometry of species distributions at multiple spatial scales

David Storch,[1,2]***** **Arnošt L. Šizling,**[1,3] **Jiří Reif,**[2] **Jitka Polechová,**[1,4] **Eva Šizlingová**[5] **and Kevin J. Gaston**[3]

[1]*Center for Theoretical Study, Charles University, Jilská 1, 110 00 Praha 1, Czech Republic*
[2]*Department of Ecology, Faculty of Science, Charles University, Viničná 7, 128 44 Praha 2, Czech Republic*
[3]*Biodiversity & Macroecology Group, Department of Animal & Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK*
[4]*Biomathematics & Statistics Scotland, University of Edinburgh, JCMB, The King's Buildings, Edinburgh EH9 3JZ, UK*
[5]*Department of Philosophy and History of Science, Faculty of Science, Charles University, Viničná 7, 128 44 Praha 2, Czech Republic*
Correspondence: E-mail: storch@cts.cuni.cz

Abstract

There have been several attempts to build a unified framework for macroecological patterns. However, these have mostly been based either on questionable assumptions or have had to be parameterized to obtain realistic predictions. Here, we propose a new model explicitly considering patterns of aggregated species distributions on multiple spatial scales, the property which lies behind all spatial macroecological patterns, using the idea we term 'generalized fractals'. Species' spatial distributions were modelled by a random hierarchical process in which the original 'habitat' patches were randomly replaced by sets of smaller patches nested within them, and the statistical properties of modelled species assemblages were compared with macroecological patterns in observed bird data. Without parameterization based on observed patterns, this simple model predicts realistic patterns of species abundance, distribution and diversity, including fractal-like spatial distributions, the frequency distribution of species occupancies/abundances and the species–area relationship. Although observed macroecological patterns may differ in some quantitative properties, our concept of random hierarchical aggregation can be considered as an appropriate null model of fundamental macroecological patterns which can potentially be modified to accommodate ecologically important variables.

Keywords

Biodiversity, biogeography, generalized fractals, Hubbell's neutral theory, macroecology, null models, scale, species spatial aggregation, species-abundance distribution, species–area relationship.

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INTRODUCTION

Several patterns in ecology that concern species richness, the abundances of species and the spatial distribution of individuals, seem to be near universal regardless of taxon and spatial scale. Macroecology has been defined as the study of such statistical regularities (Brown 1995; Maurer 1999). In the course of the exploration of the details of these patterns, the field has generated a multitude of hypotheses trying to explain each of them individually (for reviews see Gaston & Blackburn 2000; Storch & Gaston 2004; Gaston *et al.* 2008) but, since many different processes can lead to very similar patterns, these are often difficult to test. Moreover, the ubiquity of major macroecological patterns suggests that there are some more general principles behind particular biological processes which go beyond the

intricacies of a given taxon or environment, and whose nature is essentially mathematical or statistical (see Nekola & Brown 2007).

During the last two decades, it has become clear that many macroecological patterns are tightly connected, and can often be mathematically derived from each other. Some of these connections are deterministic, and particular patterns can be considered as simple by-products of other patterns. For example, the species–area relationship can be derived exactly from knowledge of the relationship between area and the probability of occurrence of individual species (hereafter the *P*–area relationship; Coleman 1981; Šizling & Storch 2004), and the slope of the species–area relationship is in turn related to patterns of species spatial turnover (Harte & Kinzig 1997) and to the relationship between local and regional species richness (Rosenzweig & Ziv 1999;

Bartha & Ittzés 2001). Other connections between macro-ecological patterns are less straightforward, with some only constraining the possible forms of others. The positive relationship between abundance and range size (Brown 1984) is, for example, almost inevitable if the spatial distributions of species are aggregated (Hartley 1998; Holt *et al.* 2002) and reveals particular patterns of occupancy at different scales (Harte *et al.* 2001). Although in most cases we do not know which patterns are primary, and which only derived (Fig. 1) – and in most cases this question does not even make sense – the knowledge of such links is extremely useful, as it allows us to determine which patterns are just necessary consequences of geometric relationships and to focus on more biologically interesting phenomena.

The finding that major macroecological patterns of species abundance, distribution and richness are mathematically tightly related has led to the idea that all of them could in fact represent different projections of one fundamental principle concerning the distribution of individuals of various species and size classes on many spatial scales, and that all of them can be derived using one universal theoretical framework. There have been several attempts to build such a framework, i.e. to build a theory which would predict as many macroecological patterns as possible with minimum *ad hoc* assumptions (Hubbell 2001; McGill & Collins 2003; Harte *et al.* 2005). These can be considered as null models, as they do not include any particular taxon-specific or environment-specific information, and attempt to derive the patterns assuming that everything is random except for some very general, relatively intuitive, principles and constraints.

Here we show that the attempts to build a general theory of macroecological patterns in species abundances, spatial distributions and richness variation have one common property, namely that they explicitly or implicitly introduce the idea of species aggregation on multiple spatial scales. Then we demonstrate that the way in which individuals are aggregated on such scales is close to fractal (i.e. it can be modelled using fractal geometry), and argue that this aggregation is the key property for understanding spatial macroecological patterns. We show that realistic patterns of conspecific spatial aggregation (and thus realistic predictions of many other macroecological patterns) can be obtained by simple random hierarchical models assuming only that species occur within sub-patches that are themselves randomly nested within patches at a higher level of a spatial hierarchy. Finally, using data on bird distributions at several spatial scales we show that our null model predicts not only intraspecific macroecological patterns, including the relationship between scale and occupancy, but also multispecies patterns, including the species–area relationship and the species-abundance distribution.

THE QUEST FOR A UNIVERSAL MACROECOLOGICAL THEORY

There have been several attempts to unify macroecological patterns. In particular, three classes of models have been proposed that attempt to explain or predict universal macroecological patterns in species abundance, distribution and species richness variation within one simple, spatially explicit framework. None of these models includes any explicit consideration of ecological differences between
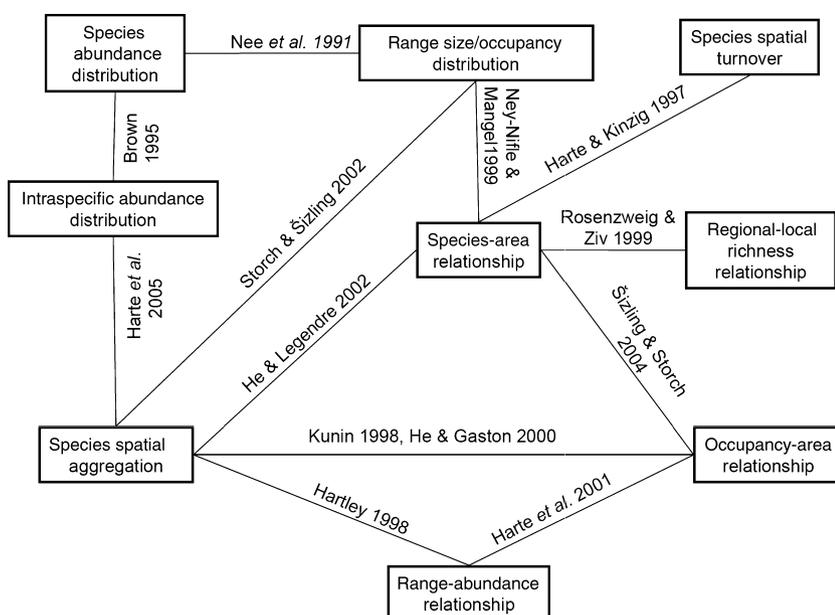
Figure 1 Links between individual macroecological patterns, revealed by different studies. The list of the links and of the studies is far from exhaustive, however, they show the interconnectedness of patterns which have traditionally been examined separately.

species in terms of body sizes or any other characteristics; they therefore concern only those patterns which we can observe using spatially explicit information on local and regional abundances of many species of a taxon or a functional group.

The models of McGill & Collins (2003) and Harte *et al.* (1999, 2005) assume a particular spatial structure to individual species distributions to explain other spatial macroecological patterns. McGill & Collins (2003) assume one or a few peaks of high abundances, which drop off rapidly with the distance from the peak to a long tail representing the majority of sites with low abundances. Harte *et al.* (1999) attempted to derive the species–area relationship and the species-abundance distribution from an assumption of a simple community-level probabilistic allocation rule which applies repeatedly at successively finer spatial scales defined by successive bisection of a given area. This model was later extended and interpreted in terms of parameters of ranges of particular species – i.e. at species level (Ostling *et al.* 2000, 2003). Although Maddux (2004) has demonstrated that this model produces biologically unrealistic outcomes (but see Ostling *et al.* 2004), Hui & McGeoch (2008) show that these problems can be solved when assuming 'heritability' of the probability of individual allocations across spatial scales. In a similar, albeit more sophisticated, model Harte *et al.* (2005) derived all the patterns of concern from the probabilistic allocation rule applied separately to each species, assuming that all numerically distinguishable states of possible allocations of individuals at a given spatial scale have equal probability (e.g. if a species has 100 individuals the probability that, for example, all would be in the left half of an area being bisected is the same as that of 50 individuals being in the left half and the other 50 in the right).

These models predict realistic parameters for the species–area relationship, the positive interspecific relationship between abundance and range size, local species-abundance distributions and patterns of species spatial turnover. However, their assumptions seem to be partially arbitrary – the spatial abundance structure of species ranges is often considerably more complicated than assumed by the model of McGill & Collins (Gaston 2003), and there is no *a priori* reason why species distributions should follow the quite specific allocation rules postulated by Harte *et al.* (1999, 2005) – and they have no direct biological interpretation (but see Harte 2007). More importantly, these models have to assume a specific species-abundance distribution for the whole region, i.e. they are actually parameterized by the observed pattern of relative species abundances.

Hubbell's (2001) neutral theory combines both evolutionary and ecological processes in one simple framework, and generates many macroecological patterns on the basis of processes of reproduction, death, colonization and specia-

tion. The neutral community dynamics consist of the replacement of dead individuals by the recruitment of randomly selected ecologically equivalent individuals from a local community or, with lower probability, from other local communities which together comprise a whole metacommunity (see also Chave 2004). The species-abundance distribution of the whole assemblage as well as the abundance structure of local communities are also determined by this process, i.e. the model does not need an *ad hoc* parameterization in terms of any species-level properties. However, it requires fine tuning of parameters determining the dynamics, namely migration and speciation rates, to produce realistic macroecological patterns, and spatially explicit realizations of the model also require characterization of the dispersal kernel to produce spatial patterns including the species–area relationship (Borda-de-Água *et al.* 2007).

All the theories mentioned above give generally quite realistic patterns when properly parameterized, although they differ considerably in their assumptions. It is thus natural to ask whether some more general principles could not lay behind all the patterns. Close examination of the models reveals that all have one feature in common: they introduce some form of conspecific spatial aggregation to produce macroecological patterns. In the case of the McGill & Collins (2003) model, this is performed simply by postulating peaks of high abundance and tails of low abundance across species ranges, whereas in the model of Harte *et al.* (2005) the assumption of equivalency of all numerically distinguishable states favours aggregation on all spatial scales. The neutral theory postulates that local recruitment is more probable than recruitment from distant localities, leading to the prevalence of particular species in each local community, i.e. again an aggregated spatial distribution. This effect is in fact responsible for realistic scaling of species numbers with area and the patterns of species abundance structure within the metacommunity. It is therefore reasonable to argue that the key feature responsible for most macroecological patterns of this kind is in fact conspecific spatial aggregation. Indeed, close inspection of Fig. 1 reveals that spatial aggregation has repeatedly been related to many of these patterns, and many of them have actually been derived from some simple assumptions concerning spatial aggregation (e.g. Hartley 1998; He & Gaston 2000; He & Legendre 2002; Green & Ostling 2003; Martin & Goldenfeld 2006).

CHARACTERIZATION OF SPATIAL AGGREGATION ON MULTIPLE SCALES

If spatial aggregation is the clue to a unifying framework for macroecological patterns, we can ask whether there are

some properties of aggregated distributions which would be universal and which would clarify the emergence of these patterns. One way of characterizing the spatial aggregation of a single species on multiple scales is through the *P*-area relationship, i.e. the relationship between the area of a plot and the probability of species occurrence within a plot of this area (He & Gaston 2000; Harte *et al.* 2005), or between the area of a grid cell and the proportion of occupied cells of this size (Kunin 1998; He & Condit 2007), which is an estimate of the probability of occurrence. Larger areas have a higher probability of overlapping the distribution of a species, so that the probability of species occurrence increases with the area of the sample plot (census window). However, if the distribution is relatively uniform (regular or random), the probability of occurrence is very high even for relatively small sample plots regardless of their location, whereas even large sample plots can remain unoccupied if a species' distribution is clumped. The *P*-area relationship for a wide range of areas (sizes of sample plots) thus characterizes spatial aggregation on multiple scales.

A linear increase of a *P*-area curve in a log–log space, i.e. a power-law *P*-area relationship, is characteristic for fractal sets. As reported by Kunin (1998), observed species distributions often reveal such a relationship between the area of a cell and the proportion of occupied cells, indicating that the spatial aggregation of species can be modelled as fractal, and that the spatial structure of a species' distribution is self-similar on all reasonable scales of resolution. This statement has received some support from various spatial data sets (e.g. Virkkala 1993; Ulrich & Buszko 2003), although Hartley *et al.* (2004) demonstrated considerable deviations on some scales, and He & Condit (2007) have shown that the *P*–area relationship can generally be better characterized by a slightly more complex model suggested by Nachman (1981). In fact, there is even evidence that true random fractals generated by standard algorithms (e.g. Falconer 1990) are better characterized by Nachman's model than by the power-law (He & Condit 2007), indicating that fractals may truly represent a good approximation of species spatial aggregation even if the *P*-area relationship deviates from the power-law.

Šizling & Storch (2004) have shown that the spatial distribution of central European birds is well characterized by a fractal distribution, finding that the deviation of the *P*-area relationship from the power-law is statistically indistinguishable from the deviation in the case of exact random fractals. Moreover, they obtained an accurate prediction of the shape and slope of the species–area relationship using only the two parameters that characterize the fractal properties of each species' distribution. A fractal distribution thus seems to be a useful description of the

spatial aggregation of species that forms the basis for other macroecological patterns.

Several fractal-based models have been proposed to produce macroecological patterns (e.g. Ritchie & Olff 1999; Harte *et al.* 1999), and complex spatial species distribution patterns are now regularly analysed by fractal methodology (see Hastings & Sugihara 2002), including multifractal analysis which utilizes much more detailed information about the patterns to obtain their more accurate description (Borda-de-Água *et al.* 2007). However, although there is some evidence that particular habitats have fractal properties (e.g. Peckham 1995; Storch *et al.* 2002), so far it has been unclear why species distributions should be close to fractal and what determines the parameters of fractal-like distributions. Therefore, although fractal analyses represent useful *analytical* and *descriptive* tools, the fractal distribution itself does not currently provide a basis for a truly universal null theory of macroecological patterns.

FRACTAL SPATIAL DISTRIBUTIONS AS A RESULT OF A HIERARCHICAL PROCESS

Are there any clues as to why species spatial distributions resemble random fractals? Fractals can emerge in many ways, but for this purpose it is useful to see this as a hierarchical process connecting sequential spatial scales (hereafter, aggregation levels; see Fig. 2). The original patch is replaced with several smaller sub-patches according to a particular rule, these are then in turn replaced by yet smaller sub-patches at the following aggregation level according to the same rule, and so on (Fig. 2). It is relatively straightforward to interpret this process in terms of a habitat hierarchy and/or a hierarchy of species ecological requirements, in which the basic level would represent, say, the whole continent, which is divided into broadly defined habitats determined by climate, within which are sub-patches defined by substrates and geomorphology, divided into sub-patches of macrohabitat, composed from different microhabitat sub-patches and so on (see Kolasa 1989). Although in mathematical fractals this division goes to infinity, in the real world, it must end at some basic area unit, such as the home range of an individual (and thus the number of hierarchical steps can be dependent on the life history and body size of a species). Regardless of how individual species discriminate their habitats (certainly differently than we do), it is reasonable to assume that the nature of habitats is hierarchical, as the presence of a particular habitat type suitable for a species is always dependent on a combination of conditions, some of which (e.g. climate or geology) vary on a broad scale. The occurrence of a specific habitat is thus constrained by the presence of a more broadly defined environment (Kolasa
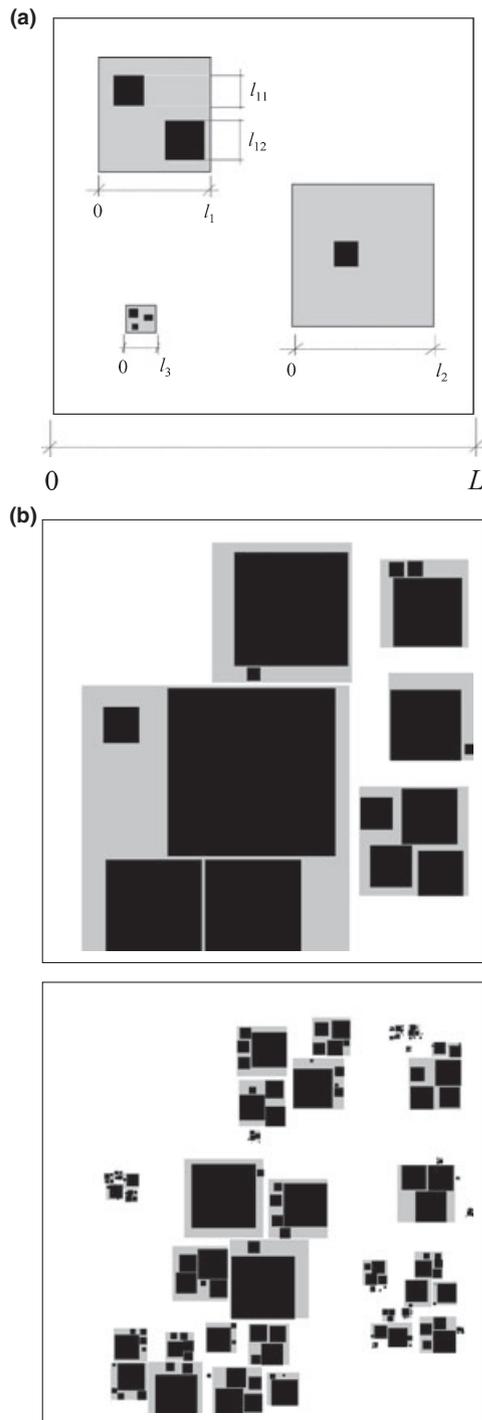
Figure 2 Emergence of a generalized fractal as a random hierarchical process. (a) The original square-shaped patch of side length L is replaced by a set of smaller sub-patches of side length l_i according to particular rules relating the areas and numbers of the sub-patches to the area of the original patch (see the text). This process continues for several aggregation levels (b), here the first and second (above) and third and fourth (below) aggregation levels are shown for one realization of the model M2 in which $r = 0.67$ (see the text).

1989; Ritchie & Olff 1999; see also Lennon *et al.* 2007), which leads to the natural habitat hierarchy and spatial clustering of specific habitats.

The idea of a habitat hierarchy explains the aggregated structure of species distributions at all spatial scales. However, it does not itself ensure the regularity (i.e. scale invariance) of the patterns obtained, which is characteristic for fractals. The problem is that the form that the replacement of patches by sub-patches can take is quite restrictive for fractals. This is a consequence of the condition of measurability under mathematical models (for details see Šizling & Storch 2007). According to the only definition that deals with the dimension of fractal structures that need not necessarily be generated by infinite processes (Mandelbrot 1977),

$$\sum_{(i)} l_i^D = L^D \tag{1}$$

where L is the length of the side of an original square-shaped patch (see Fig. 2), l_i is the length of the i-th sub-patch, and D is the dimension (either Hausdorff dimension or box dimension, with eqn 1 holding for both; see Falconer 1990). According to Mandelbrott (1977), the dimension is constant for all patches and their sub-patches at all spatial scales for fractals, and this property has been retained in all ecological applications of fractal geometry (see Hastings & Sugihara 2002; Halley *et al.* 2004). However, there is in fact no biological reason why we should find structures in nature for which D is kept constant (Šizling & Storch 2007; see also Hartley *et al.* 2004), although a constant D is undoubtedly a mathematically useful property of fractals. Moreover, structures with constant D reveal biologically untenable properties, namely the strong dependence of the total occupied area at a given aggregation level on the number of sub-patches. For example, holding $D = 1$ and altering the number of sub-patches between 2 and 3, the total occupied area alters between one-half and one-third of the area of the original patch (assuming sub-patches of equal size to simplify the reasoning). This is obvious when setting $l_i = L/2$ and $l_i = L/3$ for all i in eqn 1 [i.e. $(L/2)^1 + (L/2)^1 = L^1$ and $(L/3)^1 + (L/3)^1 + (L/3)^1 = L^1$, respectively], which implies occupied areas of $2(L/2)^2 = L^2/2$ and $3(L/3)^2 = L^2/3$ respectively. As a consequence, two structures with the same dimension may vary considerably in their P–area relationships – which is the actual driver of many macroecological patterns – depending on the number of sub-patches.

For these reasons, we release this condition and model the hierarchical process outlined above in a way which is more readily interpretable in terms of possible underlying processes, and which is at the same time less restrictive than the emergence of random fractals, using the idea we term 'generalized fractals' (Šizling & Storch 2007). It is based on

an assumption that the proportion of area occupied at a particular aggregation level is biologically more important and better interpretable than the fractal dimension *D*. Indeed, the proportion of occupied area is directly related to the probability of occurrence, and can thus be directly translated to the *P*-area relationship.

THE IDEA OF GENERALIZED FRACTALS

The generalized fractal can be defined as any structure which emerges by the hierarchical process that comprises the replacement of patches of the original pattern with any patchy pattern formed by any particular process repeated on many scales (see Šizling & Storch 2007, for more formal definitions and mathematical rationale for this generalization of the idea of fractals). Generalized fractals thus represent the most general way by which to produce structures that are aggregated on many scales of resolution, although their realizations differ, depending on whether this process is entirely random or constrained in some way. Classical random fractals represent just one possible realization of generalized fractals, in which the process is constrained by the necessity of keeping the dimension *D* constant for all patches and all aggregation levels. A biologically more plausible possibility is that, instead of *D*, it is the proportion of an area which is covered by all sub-patches that is similar for all aggregation levels. This would suggest some species-specific scale-invariant property enabling the occupation of space, potentially interpretable in terms of species niche width and/or correlated with some species feature. Alternatively, if this proportion was similar (or, in the extreme, constant) for all patches within a given aggregation level but varied among the levels, this would suggest ecological properties which are spatially autocorrelated but scale-specific. Finally, the proportion could also be completely random, varying both in space and across spatial scales, suggesting factors or processes operating independently within each patch and at each spatial scale (Box 1).

Whichever approach is more realistic, the proportion of an area covered by sub-patches seems likely to be a more important parameter in shaping species distributions than does *D*. However, since we cannot *a priori* evaluate the biological realism of the three distinct possibilities (all of them seem potentially to be biologically interpretable, although the interpretation is never straightforward), we decided to make models of generalized fractals that are as general as possible, exploring the whole space of possibilities, and assuming that reality lies somewhere within this space. In fact, species spatial aggregation is not only related to habitat structure, but is also produced by spatial population and metapopulation processes (e.g. Storch *et al.* 2003), and we can assume that these processes will be more important than habitat structure at some scales. However, generalized fractals modelled in this way represent a universal approach to any multi-scale aggregation, regardless of its precise biological causes.

There are many ways in which generalized fractals, as defined above, can be realized and modelled. Hereafter, we will deal with those which can be characterized by the equation

$$\sum_{(i)} \left(\frac{l_i}{L} \right)^D = r \tag{2}$$

where either (i) *D* varies between 0 and 2 among species (individual realizations of generalized fractals) and *r* (relative occupancy within an aggregation level) is equal to 1 (i.e. classical random fractal), or, alternatively, *D* is equal to 2 and *r* is either (ii) constant for all patches and all aggregation levels for a given species, (iii) varies among aggregation levels, or (iv) varies randomly among all patches within all aggregation levels. In all cases, we have only one driving parameter, *r* or *D*. Such an approach enables several types of generalized fractals (including classical random fractals) to be modelled using the same algorithm but different parameters, so that different models can be directly compared to each other. Note that the variation in *r* cannot be substituted by the variation in *D*, as these parameters are actually independent if the number of sub-patches is not constant – for a given *D* the proportion of occupied area within the patch *r* can freely vary between 0 and 1 (see above).

As in the case of classical random fractals, the process of patch division can potentially continue to infinity, which is clearly biologically unrealistic – the number of levels of aggregation is constrained at least by the home range of the respective species. For comparison with any real data set, it is necessary to use a sufficient number of levels of aggregation to produce patches which are smaller than the basic resolution of the data (e.g. size of a grid cell). In such a case, the basic grid cell can be considered as occupied regardless of the size of a respective patch at the final level of aggregation (i.e. even if final patches are much smaller). Most macroecological patterns are based on species occupancy patterns measured at a given resolution (grain), and are not affected by patterns occurring at a yet finer resolution. The obvious exceptions concern abundance patterns. Here we will assume that abundance converges to occupancy at a grain size corresponding to the average size of home ranges, and thus we model generalized fractals with the aim of producing patches at the final level of aggregation which are smaller than this grain size (see below), and consider the final patch size as corresponding to the resolution of the measurement.

**Box 1: Habitat hierarchy and the meaning of *r***

Imagine a species of, say, phytophagous insect, which is dependent on one host plant species growing in a certain type of mountain forest. The first level of aggregation, i.e. the broadest habitat description, then comprises mountain ranges. Depending on the location of the whole study area, mountains can cover any part of it, i.e. the area of mountains is expected to be anything between zero and the whole area in question. Also, it is expected that there can be several mountain ridges, so that the number of habitat patches (i.e. sub-patches of the whole area) may vary. The same applies for the second aggregation level: if we do not assume any particular biological processes, we should consider all the possible proportions of the forest type within the mountains as equivalent. Similarly, the host plant may be rare as well as widespread within the given forest type. Finally, the distribution of the insect may be patchy even within the area defined by the presence of the host plant, depending on its spatial (meta)population dynamics. In this example we consider four levels of aggregation, but the number of these levels may apparently vary from species to species.

The truly null expectation, corresponding to our last model, M4 (see the model descriptions), is that the proportion *r* is random for every habitat patch. However, in reality, *r* can be quite similar in different places. For instance, if the proportion of aspen forest is *c.* 0.3 within a given mountain ridge, it is probably similar on another ridge, although the level of similarity depends on the similarity of altitudinal range and other factors between the two mountain ridges. In the extreme (our model M3), we can assume that *r* is constant across different locations within a given level of aggregation, representing spatially autocorrelated processes which determine habitat occurrence within more broadly defined habitats.

Furthermore, we can assume that the proportion *r* will be somehow propagated through different levels of aggregation, as modelled by constant *r* across scales in our model M2. Imagine a generalist species, associated with a wider range of host plants. In such a case, some host plant species can occur even in particular lowland

habitats (*r* for the first level of aggregation is thus higher than in the previous case), and within both mountain and lowland habitats they can grow in several forest types (higher *r* for the second aggregation level). More host plant species together form larger patches of suitable habitat within respective forest types, which may be followed by higher relative occupancy at the finest level of aggregation (e.g. due to the stronger rescue effect, Brown & Kodric-Brown 1977), reflected by higher *r* for the third and fourth aggregation levels. Niche breadth may thus affect *r* in a similar way on several scales.

It is probable that reality will lie somewhere between these possibilities, i.e. *r* will not be completely independent in all patches and scales, nor the same across all levels and patches. Our comparisons of the models with data (see Results and Figs 3–6) show generally (although not always) better fit of models M3 and M4, indicating that the propagation of *r* across scales is weaker than its spatial correlation. This is in accord with the general notion that habitat distribution can have very different causes at different spatial scales (and levels of habitat hierarchy) but these effects act in a similar way in different locations. The three models thus simply delimit the space of all possible hierarchically aggregated structures, and their overall good fit indicates that it is the multi-scale aggregation itself and not a particular mechanism which is responsible for general features of macroecological patterns.
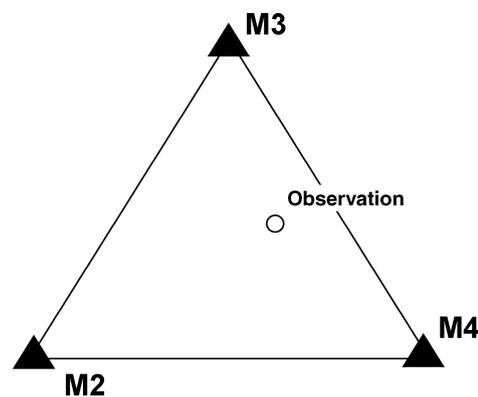
TESTING THE MODELS OF GENERALIZED FRACTALS

The data

Analyses were conducted using three data sets on observed bird distributions:

(1) A square of 16 × 16 contiguous mapping quadrats from the breeding bird atlas of the Czech Republic (CR), each

quadrat spanning 6′ latitude and 11′ longitude (i.e. *c.* 12 × 11.1 km) and containing records of the presence of all species with confirmed or probable breeding during the period 1985–1989 (Šťastný *et al.* 1996; see also Šizling & Storch 2004 for details).

(2) A square of 16 × 16 mapping quadrats within central Europe (CE), taken from the European breeding bird atlas (Hagemeijer & Blair 1997); each quadrat was ca 50 × 50 km, and also contained presence/absence data

for breeding species (see Storch & Šizling 2002; Šizling & Storch 2004).

(3) A linear transect of 768 mapping points, separated by *c.* 400 m, across the whole territory of the Czech Republic (Transect), at which all birds were mapped by D.S. and J.R. using the point count method (Bibby *et al.* 1992) limited to a maximum distance of 150 m around each point. Birds were mapped during five early morning visits in the breeding seasons (April–June) of 2004 and 2005, and the maximum recorded numbers of individuals of each species from the five visits were then taken for every point (see Storch *et al.* 2002). This data set is therefore at a considerably finer spatial resolution than the previous ones, and also contains information on species abundances.

The models

We performed four simulations for comparison with each data set, differing in the constraints determining the spatial patterns generated, with simulations for the atlas data also differing slightly from those for the transect data. All the simulations followed eqn 2 and an identical algorithm, so that their outputs were fully comparable with each other. In the construction of species assemblages we assumed completely neutral interactions between species, i.e. we overlaid spatial patterns for different species without assuming any interdependence among them. Species' spatial distributions were modelled as the spatial arrangement of patches (for convenience, squares) at the final aggregation level. The simulations were as follows:

M1 – simulation of the fractal model. This procedure generates random fractals, producing patchy structures, which keep D constant over all aggregation levels (Mandelbrott 1977). At each aggregation level, each square was replaced by several smaller non-overlapping squares of randomly varying sizes and locations (see below) so that D remained the same (see eqn 1). D was drawn from the observed distribution of values for individual species; $r = 1$. This process was repeated for four aggregation levels.

M2 – simulation with fully correlated r (i.e. r constant for a given species across space and spatial scales). The original square was replaced by a set of n non-overlapping squares randomly varying in size, whose total area represented a proportion r of the original square, r being randomly selected from a uniform distribution between 0 and 1 for each species; $D = 2$. This procedure was repeatedly applied to each square again for four aggregation levels.

M3 – simulation with only spatially correlated r. Here the procedure was the same as in the previous case, but

r varied randomly for each aggregation level, i.e. r was randomly drawn from the uniform distribution separately for each aggregation level; $D = 2$.

M4 – simulation with completely uncorrelated r. In this case, r varied not only between aggregation levels, but randomly for each individual square – the total proportion occupied by smaller non-overlapping squares within a square varied randomly between squares in each aggregation level as well as between levels; $D = 2$.

We constructed one assemblage of 200 species for comparison with the atlas data sets and a set of 10 assemblages (each of 144 species) for comparison with the transect data (see below) for each model. The macroecological properties of the assemblages resulting from simulations M1–M4 were compared, and these properties were contrasted with those of the real assemblages of central European birds censused on the three spatial scales. To compare the models with the observed data at the finest spatial scale, the linear transect, we overlaid the two-dimensional spatial structures produced by the models with the map of the transect of census points and recorded the presences of all species whose modelled ranges overlapped respective points (i.e. the circles of 300 m in diameter). To compare the models to the atlas data at the larger spatial scales, we overlaid each modelled range with a grid of 16×16 cells and again censused modelled species presences. Transects as well as grids were located in central parts of the modelled area, to avoid edge effects.

Model construction procedure

To produce generalized fractals representing aggregated structures, it is necessary to divide each patch into relatively few sub-patches, because too many small patches would lead to a rather homogeneous spatial distribution and extremely small patches at the final level of aggregation. In the model used for the comparison with atlas data, we divided the initial patch (i.e. the whole study area) into a random number of square-shaped cells between 2×2 and 5×5, and then we randomly placed one or no square of random size (between zero and the cell size) into each cell (see Šizling & Storch 2007). The only condition held was eqn 2 for each replacement; therefore, each cell was finally either empty or occupied by just one square of random size and random position. This simulation is biased toward a slight regularity in spatial distribution of the squares (patches), which affects earlier saturation of species–area relationships.

In the models used for the comparison with the transect data, the number of patches (again modelled as squares) at each step varied at random between two and five. The sizes of the patches l_i were drawn from a uniform distribution and

were constrained by eqn 2 and by ensuring that all patches could in principle fit into the area with a side length $L = 1$. The two largest patches were then placed so that they both fit into the unitary area, then the algorithm randomly placed every further patch into the remaining available space, and the set was discarded if not all patches could be placed. We checked for the distributions of patch sizes in the output sets. The output distribution of patches was unbiased for approximately $r < 0.5$, $D = 2$ and $D < 0.9$, $r = 1$. When the covering was denser, however, the output distribution was not uniform but biased with more small and very large patches – note that for D near two and r near one the whole area is almost completely filled, which can be realized only by a set of a large square and several very small ones or possibly with four almost equal-sized squares – hence the distribution is necessarily biased. We redrew the patch sizes if the allocation of all of them was unsuccessful five times. If the cycle failed to find placement of all patches for more than a hundred times for a given r or D (large), a lower number of patches was accepted.

For each of the four levels of aggregation, the new sets of patches were generated using the above procedures, and rescaled according to their respective 'parental' patch in both cases (each patch becomes the 'unitary area' in the above algorithm). The structure of a species distribution thus has four aggregation levels.

Macroecological patterns

With the exception of patterns related to local species coexistence (e.g. community nestedness), which obviously cannot be predicted by models assuming the complete independence of species spatial distributions, many quantities that could usefully be measured from the model results and the observed data are mathematically related to each other (Fig. 1, see Harte *et al.* 2005). We therefore explored four quantitative properties which sufficiently characterize the structure of species assemblages, and at the same time are more or less independent from each other:

(1) The P-area relationship for all species, calculated as the relationship between the area of a plot (or the length of transect) and the probability that the plot will be occupied by the focal species. By 'plot' we will mean any particular square comprising a given number of unit quadrats, or a line segment comprising a given number of points, respectively. The probability was calculated as the proportion of occupied plots from all possible plots of a given area (or length). We evaluated the shape of the observed or modelled P-area relationship by estimating the deviation from the power law P-area relationship (i.e. the P-area relationship that is linear in log–log space). The deviation (hereafter ε) was calculated for each area

(measured in number of unit quadrats or points respectively) as the difference between the probability of occurrence calculated using the power-law function approximating the P-area relationship truncated by the point of saturation (the area where $P = 1$) and the probability of occurrence predicted by each model or observation (Šizling & Storch 2004).

(2) The frequency distribution of box dimensions (Mandelbrott 1977; Falconer 1990; Šizling & Storch 2004) of the spatial distribution of each species (except for model M1 in which this distribution was set to follow that observed). The frequency distribution was expressed as the relationship between species rank and the box dimension.

(3) The species–area relationship for the whole assemblage, measured as the relationship between area or length (expressed again in the number of unit quadrats or points, see above), and the mean number of species in all possible plots of this area (Šizling & Storch 2004).

(4) The distribution of species' occupancies at the finest scale. The distribution of number of quadrats occupied by individual species depends on the spatial resolution (Kunin 1998), and species occupancy approaches species abundance if the units approach the approximate size of a home range or a minimum distance between neighbouring individuals. Since we deal with species whose home ranges approach the basic spatial units of transect (most points were occupied by just one individual of most species and there were no individuals that shared two or more points), we assume that the distribution of occupancies is close to the species-abundance distribution at that scale. We therefore focused on the finest spatial resolution possible, using only the transect data for comparison with the models.

RESULTS

The P-area relationship for modelled and observed atlas data deviates significantly ($P < 0.01$) from the straight line on a log–log scale expected from the power-law, though the absolute value of the deviation is relatively small (mean absolute deviation, $|\varepsilon|, < 0.04$; Fig. 3a) and comparable in all cases. Moreover, the deviations derived from the observed data are more variable than those from the models of generalized fractals, with the latter falling mostly between those for the CR data on the one hand and the CE data on the other. Note that fractal distributions (model M1) reveal similar deviations ($\max|\varepsilon|$) from a linear P-area relationship as do other models and the observed data. The deviation from the power-law differs between the modelled and the observed transect data (Fig. 3b), although the overall trend
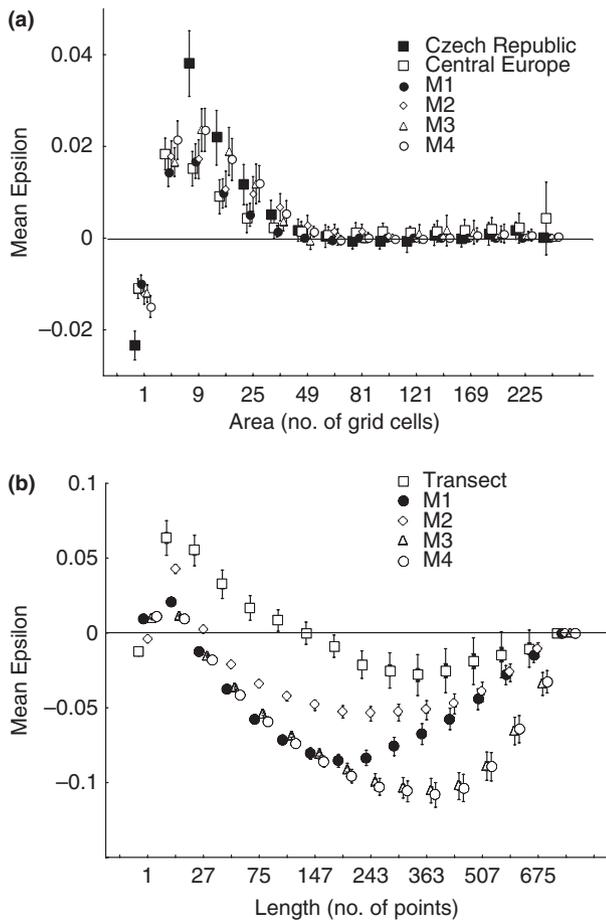
Figure 3 Mean deviation from the power-law *P*–area relationship (mean epsilon) for all of the models and the observed (a) atlas data and (b) transect data. ε was calculated for each area as the difference between the probability of occurrence calculated as the power-law truncated by the point of saturation (the area where $P = 1$) and the probability predicted by each model or observation (see Šizling & Storch 2004). Mean (marks), $CI_{0.5}$ (boxes mostly hidden behind marks) and $CI_{0.95}$ (whiskers) of the mean epsilon are shown.

and maximal deviations are similar. The models thus do not lead to the exact power-law *P*-occupancy relationships for individual species, but their deviation from the power-law is comparable to that of observed spatial distributions of species.

The frequency distributions of box dimensions, as reflected in the relationship between species rank and the box dimension, are similar for all modelled and observed assemblages (Fig. 4a,b). As in the case of the *P*-area relationship, the observed distributions for the CE and CR data actually represent the extremes of all of the distributions, with the modelled distributions falling somewhere in between. The distribution of box dimensions produced by model M2 seems to be closest to those
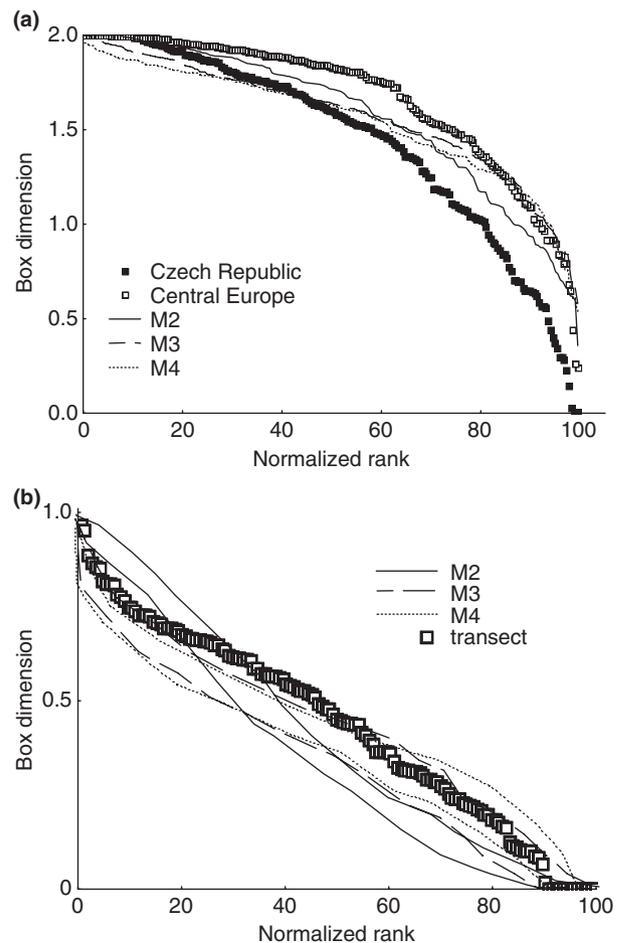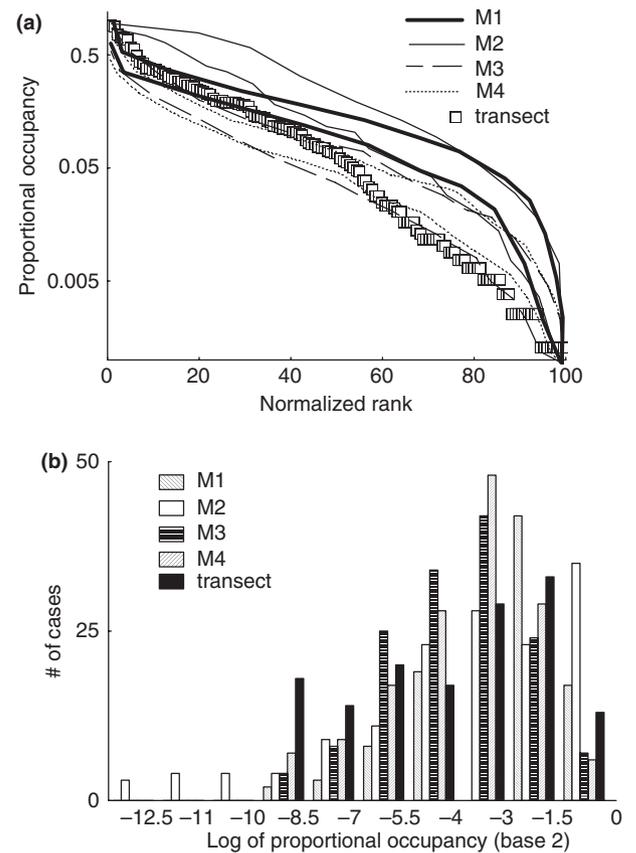

Figure 4 Frequency distribution of box dimensions revealed by the relationship between species rank and box dimension for observed species spatial distributions and all models except M1 which had to be parameterized by the observed distribution of box dimensions; (a) atlas data, (b) transect data (the results of M4 nearly overlaps those for M3). Outlines of 10 simulation runs are shown for the models in (b).

observed for the CR and CE data, whereas the distribution for the transect data is very close to those produced by models M3 and M4 (Fig. 4b; distributions produced by models M3 and M4 overlay each other). When the match between modelled and observed distributions of box dimensions using the transect data was tested using Kolmogorov–Smirnov (K–S) statistics (Dvoretzky–Kiefer–Wolfowitz, DKW, test), those generated by the model with fully correlated *r* (M2) were rejected ($P < 0.05$; $K–S > 0.1$; $N = 144$) in eight cases from 10, whilst the other models could not be rejected at all. The models of generalized fractals therefore predict well the assemblage-wide patterns comprising interspecific variation in the structure of spatial distributions, without any *ad hoc* assumption concerning these distributions.

(a)

(b)
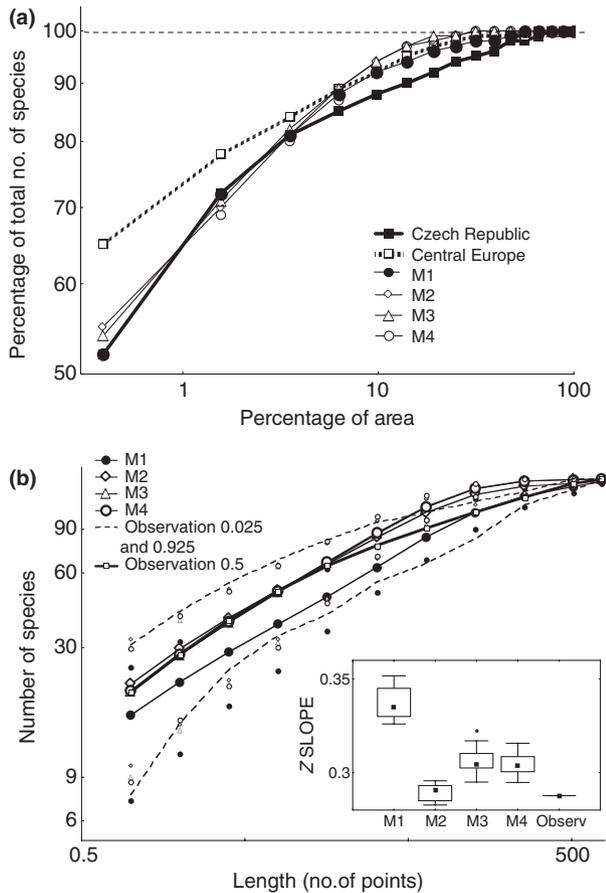
Figure 5 Increase of species richness with (a) area and (b) the number of consecutive points on the transect for modelled and observed assemblages (both axes are logarithmically transformed). Mean values of observed species richness and of species richness from one model realization are shown in (a). In (b) the thick line refers to the median and dashed lines to $CI_{0.95}$ of observed species richness values; large marks connected by solid lines refer to median values for simulations, whereas small marks refer to $CI_{0.95}$ of simulated species richness. The inset shows the distribution (squares – medians, boxes – $CI_{0.5}$, and whiskers – $CI_{0.95}$) of the slopes of the regression lines of all species–area relationships.

(a)

(b)

Figure 6 Distribution of relative occupancies at the smallest scale, where it approaches the species-abundance distribution, for the transect data and the four models. (a) is the rank-occupancy/abundance plot showing outlines of 10 realizations of each model; (b) is the histogram of the logarithmized occupancy/abundance values showing the results of one randomly selected realization of the models.

The exact shape of the species–area relationship differs between the observed atlas and transect data, as well as between the respective models (Fig. 5a,b). For atlas data (Fig. 5a), all the models produce very similar species–area relationships revealing saturation at very large areas, which could be attributable to a bias towards regularity in the spatial distribution of sub-patches within a patch at these scales, introduced by the algorithm used for the construction of these distributions (see Šizling & Storch 2007). However, the slope of the curve below the point of saturation, ranging between 0.15 and 0.17, corresponds very well both to the observed slopes (0.1 and 0.12 for CE and

CR, respectively), and to the values most commonly reported for mainland species–area relationships (Rosenzweig 1995; but see Drakare *et al.* 2006). For the transect data, the modelled slopes differ slightly between the models (0.32–0.35, 0.28–0.29, 0.29–0.32 and 0.29–0.32 in M1, M2, M3 and M4, respectively), although they are all close to the observed slope of 0.29, and the 95% confidence intervals of observed species numbers overlap with mean species richness values for modelled assemblages (Fig. 5b).

Species occupancies at the finest spatial scale modelled and observed on the transect have unimodal, albeit somewhat left-skewed, distributions when the occupancies are log-transformed (Fig. 6). This is also the most commonly reported form of observed species-abundance distributions (Tokeshi 1999; Gaston & Blackburn 2000; Hubbell 2001; McGill *et al.* 2007). The distribution of species occupancies differs between individual models, and the predicted distributions differ from that observed on the transect (Fig. 6a), but the

overall agreement is surprisingly high (DKW test for K–S statistics: M1 rejected at level 0.03, M2 rejected in one simulation out of 10 at level 0.05, and M3 and M4 cannot be rejected). None of the models predicts the observed pattern without some bias. Part of this bias follows from the fact that in reality r is neither fully uncorrelated nor fully correlated across space and aggregation levels (see Box 1).

DISCUSSION AND CONCLUSIONS

The generalized fractals that emerge from a random hierarchical aggregation process represent a very good approximation to observed species spatial distributions. Interestingly, models differing in the particular form of this randomness do not differ too much in the properties of the spatial structures that they produce (see also Šizling & Storch 2007). Apparently fractal spatial distributions so far reported for many species (Virkkala 1993; Kunin 1998; Ulrich & Buszko 2003) can thus in fact reflect the outcome of a random aggregative process which can be quite broadly defined. Such a process can be interpreted in terms of a habitat hierarchy, leading to the situation in which patches that determine the distributions of species are more or less randomly nested within patches at higher levels in the hierarchy. In fact, the process can be much less random, which is then expressed in the deviation from the null pattern predicted by the model. Indeed, the observed macroecological patterns revealed higher variation than the models, indicating that the latter represent a null expectation when particular biological processes do not bias the mean behaviour.

It is not particularly surprising that the random models produce the patterns which are most commonly observed in nature regardless of taxon and ecosystem specificities – the fact that they are universal means that the intricacies of a given biological situation cannot play a role in their emergence. In other words, our focus on universal macroecological patterns determines the level of generality of underlying processes. Whereas the tendency for aggregated distributions at multiple scales seems to be universal across all living forms (e.g. Condit *et al.* 2000), and thus represents the basis of the general form of macroecological patterns, the exact way in which species are spatially aggregated, and the strength of this aggregation, is determined by species' biological properties, population dynamics and interactions with particular environments.

Since our models produced quite realistic macroecological patterns on the basis of a very broad range of hierarchically aggregated spatial structures without assuming any interspecific interactions, it is most probable that it is indeed the aggregated nature of species spatial distributions on multiple scales which lies behind many such patterns of abundance,

distribution and diversity. Spatial aggregation is also the characteristic property of other theoretical frameworks attempting to unify macroecological patterns. It is possible that the other approaches, including the models of McGill & Collins (2003), Harte *et al.* (2005) or Hubbell's neutral theory, could produce very similar aggregated structures, and could then represent just an alternative way of producing realistic aggregated distributions and consequent macroecological patterns.

This said, we feel that our approach has some advantages over these others. First, it explicitly and directly considers the proximate driver of the respective macroecological patterns (i.e. aggregated species' spatial distribution over multiple spatial scales), and provides a mechanism producing aggregated spatial distributions which is biologically interpretable in terms of a habitat hierarchy. Second, it does not need any *ad hoc* parameterization to obtain patterns that qualitatively and often also quantitatively represent well those most commonly observed; even species abundance patterns follow from the hierarchical aggregation. Third, it does not need an assumption of ecological or demographic equivalency among species; instead, it assumes that species differ in ecologically relevant properties, and these differences can be modelled by a random process – the 'random variation' of r can in fact reflect biologically relevant life-history characteristics.

Our approach sheds light on a continuing discussion concerning the scale-dependency of ecological patterns and processes. On the one hand, there is a claim that different processes act at different scales and hence a true understanding of nature must encompass these scale differences (Allen & Starr 1982). On the other hand, the scaling approach tries to find properties which are scale-invariant, knowledge of which would allow us to predict behaviour and patterns at a specific scale from knowledge of the parameters at another scale (e.g. Kunin 1998; Kunin *et al.* 2000). We show that these two approaches are actually compatible. Different spatial scales can indeed differ in terms of the dominant processes, but there can still be some features which are scale-independent, even if these are only statistical in nature. Understanding such statistical invariances can lead to predictions of general properties apparent across scales, although deeper biological understanding is necessary for the description of scale-dependent processes.

Our null model of macroecological patterns could in principle be modified to accommodate more biologically relevant processes and to narrow the scope of predictions for a particular situation. For instance, r could vary according to levels of available energy, thus predicting the response of species distributions to the energy availability gradient. Bonn *et al.* (2004) have shown that higher species richness in more productive areas is associated with higher

mean occupancy of all species, and this in turn affects the slope of the species–area relationship (Šizling & Storch 2004; Storch *et al.* 2005). It is possible that all of these patterns could easily be modelled by systematic changes in *r* across space, which can be interpreted in terms of varying resource levels which are sufficient for population persistence. Similarly, climatic changes can have a profound effect on *r*, both in terms of its mean value and its statistical distribution, consequently affecting all assemblage-level macroecological properties. Our model could then be useful both in the context of theories dealing with spatial variation in species richness (see Evans *et al.* 2005; Storch *et al.* 2006) and for the prediction of changes in species assemblages related to global climate change. At the same time, the deviations from our model may be indicative of biologically important processes which go beyond the statistical regularities revealed by macroecological patterns.

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