

# Fractal species distributions do not produce power-law species-area relationships

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We derive the species-area relationship (SAR) expected from an assemblage of fractally distributed species. If species have truly fractal spatial distributions with different fractal dimensions, we show that the expected SAR is not the classical power-law function, as suggested recently in the literature. This analytically derived SAR has a distinctive shape that is not commonly observed in nature: upward-accelerating richness with increasing area (when plotted on log-log axes). This suggests that, in reality, most species depart from true fractal spatial structure. We demonstrate the fitting of a fractal SAR using two plant assemblages (Alaskan trees and British grasses). We show that in both cases, when modelled as fractal patterns, the modelled SAR departs from the observed SAR in the same way, in accord with the theory developed here. The challenge is to identify how species depart from fractality, either individually or within assemblages, and more importantly to suggest reasons why species distributions are not self-similar and what, if anything, this can tell us about the spatial processes involved in their generation.

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One of the major goals of ecology is to describe and understand patterns in species' spatial distributions, both as individual species incidence and the emergent properties of assemblages (Brown 1995). The spatial structure of species' distributions has long been described in terms of species-area relationships (SARs), with an as yet unresolved debate about the nature of this relationship and the processes involved in the generation of the different types of SAR observed in nature (Arrhenius 1921, Gleason 1922, Connor and McCoy 1979, Williamson 1988, Rosenzweig 1995, Lomolino 2000). The classical power-law SAR (Arrhenius 1921) is usually taken as the point of departure in discussions of SARs.

Of course, theory is important here. Recently, it has been argued that if individual species in an assemblage have self-similar (fractal) spatial distributions, then the power-law SAR follows (Harte et al. 1999a, b). If this were true, then there would be an intellectually satisfying unity between the often reported power-law SAR

(Connor and McCoy 1979, Rosenzweig 1995), evidence that many environmental phenomena (e.g. mountains, coastlines, rivers, clouds) have fractal properties (Mandelbrot 1977, Rodríguez-Iturbe and Rinaldo 1997) and evidence that some individual species have approximately self-similar spatial distributions across scales (Williamson and Lawton 1991, Kunin 1998). Fractal spatial structure has also formed part of theories for biodiversity patterns (Ritchie and Olf 1999). Moreover, scaling properties of distributions may be of direct practical use in predicting species abundance from coverage maps (He and Gaston 2000, Kunin et al. 2000).

The main purpose of this paper is to show that, in fact, the empirical power-law SAR does not follow from fractal distributions of individual species. We derive a theoretical SAR for fractal species distributions where the box-counting fractal dimension  $D$  is allowed to vary between species, and show that this SAR is radically different from the power-law SAR. We then demonstrate that estimating the fractal  $D$  from real

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species' distributions and using these to construct a predicted SAR leads to a similar characteristic departure from the power-law SAR – and from the observed SARs of the taxa concerned. We use data for two contrasting plant assemblages (Alaskan trees and British grasses), to demonstrate the generality of these findings.

## Methods

### Self-similarity and the power-law SAR

Harte et al. (1999a, b) derived the classical power-law SAR by defining individual species with fractal spatial distributions (see also Harte 2000). However, a major assumption of their derivation is that *all species patterns have the same fractal (box-counting) dimension  $D$* . This assumption was not stated explicitly, as they derived their SAR in terms of a novel parameter  $a$ , rather than  $D$ . This parameter  $a$  was defined as the constant probability that, when an area known to contain the species is bisected, one of the halves chosen at random contains the species (obviously this has a lower limit of  $\frac{1}{2}$ ). The value of  $a$  was assumed to be identical for all species. This is the same as assuming a constant  $D$  for all species, since it can be shown that  $a$  is a function of  $D$  such that:

$$D = 2 \left( 1 + \frac{\log a}{\log 2} \right) \quad (1)$$

### What are the consequences of different fractal $D$ s?

There is a need to consider different fractal dimensions for observed distribution patterns, as there is empirical evidence that  $D$  varies between species (Virkkala 1993, Kunin 1998). For example, estimates for birds in Finland (Virkkala 1993; see also Gautestad and Myrterud 1994) show a mean  $D$  across 50 species of passerines of 1.58 with a range between 0.64 and 2 (these are the corrected values as suggested by Gautestad and Myrterud 1994).

If we have an assemblage of species with different  $D$ s, we can develop an expression for the emergent SAR (Kunin and Lennon 2001). First, consider the spatial incidence of a single fractally distributed species. We define scale fractionally, such that the scale of the whole survey area is deemed to be of unit length and area; this total area is then subject to subdivision into smaller quadrats, at finer scales. For a quadrat of side length  $s$ , the number of quadrats occupied by the species changes with quadrat size linearly on log-log axes:

$$\log n = -D \log s + \log n_0 \quad (2)$$

where  $n$  is the number of occupied quadrats,  $D$  is the box-counting (Kolmogorov) fractal dimension and  $n_0$  is a constant. The prefactor  $n_0$  is expected to be unity for an ideal fractal, but typically an empirical fit allows it to vary (Hastings and Sugihara 1993; see also Appendix 2). Currently there is some debate as to the meaning of  $n_0$  – originally, Mandelbrot (1977) seemed to suggest that this single number summarised the *lacunarity* of a fractal pattern (roughly speaking, the size distribution of 'holes' within it); more recently lacunarity has been described as a function of scale, not as a single number, and used as a general pattern analysis tool (Plotnick et al. 1996).

We can rewrite eq. 2 as:

$$n = n_0 s^{-D} \quad (3)$$

The total number of quadrats (occupied and unoccupied) at a given scale  $s$  is  $s^{-2}$ . The probability  $p$  that a quadrat of scale  $s$  contains the species is thus given by dividing the expected number of occupied quadrats by the total number of quadrats:

$$p = \frac{n}{1/s^2}; \quad p = n_0 s^{2-D} \quad (4)$$

If we have an assemblage of independently distributed species with different  $D$ s, then the expected number of species present is the sum of the probabilities of presence of each species, so the SAR is:

$$E(R) = \sum_i p_i = \sum_i n_{0i} s^{2-D_i} \quad (5)$$

Clearly, this sum only results in a power-law when all  $D$ s are identical. Although we have introduced above the assumption that species are independently distributed for pedagogical clarity, in fact this relationship (eq. 5) holds even when species distributions are strongly associated (positively, negatively, or combinations of either across different groups of species).

### The SAR when $D$ is a random variable across species

We have derived above the SAR where we know  $D$  for each species in an assemblage. We now consider the case where  $D$  is a random variable, and each hypothetical species is assigned a  $D$  at random from some frequency distribution of  $D$ s. The simplest assumption we can make about the distribution of  $D$ s across species is that all values of  $D$  between 0 and 2 are equally likely. If we make the further assumption that the intercept parameter  $n_0$  is fixed at unity for all species,

we can derive the expected number of species present in a given area. The expected number of species present is given by:

$$E(R) = \frac{R_{\max}(1 - A)}{-\ln A} \quad (6)$$

where  $R_{\max}$  is the total number of species in entire study area and  $A$  is area (see Appendix 1 for full derivation). As area approaches unity, the expected diversity approaches  $R_{\max}$ . If we wish to relax the condition that all  $n_0$ s are unity, a similar derivation is possible, but requires knowledge of the relationship (if any) between  $D$  and  $n_0$ . It would also require that the value of  $p$  in eq. 4 is constrained to the logical interval  $s^2 \leq p \leq 1$ . This is because a real species distribution cannot occupy quadrats with a probability greater than one, and a species must always occur in at least one quadrat, whatever the scale of analysis. (See Appendix 2 for further discussion.)

This fractally-derived SAR curve is more convex than the classical power-law SAR – it rises more slowly at fine scales but more quickly at coarser scales (Fig. 1). Of the four types of relationships considered by Connor and McCoy (1979) our predicted convex SAR (eq. 6) corresponds most closely to the log(species)-area model, yet this pattern was found in fewer than 12% of the studies reviewed in their paper. The remainder of the studies they considered either displayed approximately power-law SAR curves, or had relationships departing from a power-law in the opposite direction to that predicted here (e.g. species-log(area) curves, à la Gleason 1922).

### Spatial distribution data

We now take some real species distributions, estimate  $D$  and  $n_0$  for each species, and then using these values

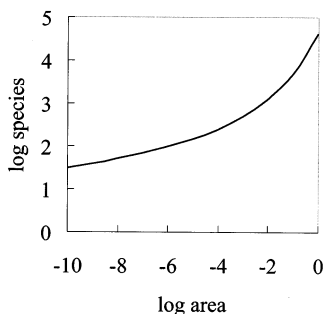


Fig. 1. The species-area relationship produced by an assemblage of species with ideal fractal spatial distributions (eq. 6 – see Appendix 1). The fractal dimension for each species is chosen at random in the interval zero to two – all dimensions are equally likely. On log-log axes, the relationship is upward accelerating, in contrast to the linear relationship produced by the classical power-law species-area relationship.

estimate the expected SAR (using eq. 5), and compare it with the observed SAR and the classical power-law curve. We use two datasets with strengths and weaknesses in different areas: one with excellent standardised recorder effort but incomplete spatial coverage, and a second with uniform coverage (an unbroken rectangle of contiguous quadrats) but more variable recorder effort. The two datasets also differ in geography (Alaska vs Britain), growth form (trees vs grasses) and species richness (8 spp vs 82 spp), to test the generality of the issues discussed here.

#### *Alaskan trees*

We used the spatial distributions of eight tree species, mapped by the United States Department of Agriculture Forest Service as part of a national coordinated survey. These data are taken from the South East Alaskan (SEAK) inventory, a comprehensive vegetation survey of 2016 fixed-area sites arranged in a lattice at 4.8 km intervals. The survey area is roughly 250 km east-west  $\times$  700 km north-south in extent, but includes substantial gaps due to the complex coastline of the region and the presence of areas which could not be surveyed for jurisdictional reasons. Each site consisted of four circular areas (radius 7.3 m), such that three were at the vertices of an equilateral triangle (of side length 36.6 m) with the fourth at the centre of the triangle. For our purposes here, we amalgamated the data from the four circular areas for each species such that a species is recorded only as present or absent in the site as a whole. Each site was surveyed using a standard field protocol by a team from the Pacific Northwest Research Station of the US Forest Service, and so the data can be considered of high and uniform quality.

#### *British grasses*

Our British grasses data were taken from the Atlas of the British Flora (Perring and Walters 1962). The distribution of each species is mapped using  $10 \times 10$  km quadrats arranged contiguously (in the scheme commonly used in Britain). We extracted data for a square region of 20 by 20 of these quadrats in the centre of Britain (south-west origin of data matrix in British National Grid coordinates at east = 330 km, north = 200 km), thereby eliminating any possibility of problems due to incorporating complex coastlines. Within this window, we excluded species present in fewer than 1% or greater than 99% of squares (such species provide little distributional information), giving a total of 82 species.

### Estimating species' fractal dimensions

There are many ways of estimating a fractal  $D$  (Hastings and Sugihara 1993, Russ 1994) but caution must

be exercised since not all methods measure the same properties of spatial patterns, and there are several different kinds of fractal dimension (Russ 1994, Falconer 1997). Indeed, the proliferation of different types of  $D$  is now a matter of some concern (Blumenfeld and Mandelbrot 1997).

For the grasses, we applied the familiar box-counting method to estimate the Kolmogorov fractal dimension  $D$  of a set of “points” (Hastings and Sugihara 1993), fitting eq. 3 by least squares regression. In practice the points are the accumulation of presence-only records, viewed through a 10 km mesh of grid squares, thus the minimum scale we considered was set by the resolution of this grid ( $s_{\min} = 0.05$ ), whilst the maximum scale was set by the extent of the study area, ( $s_{\max} = 1$ ). It is important to note that  $D$  measured in this way describes how the area of occupancy of a species’ range varies with the scale of measurement. It should not be confused with (or assumed equal to) other fractal properties of a species’ range which can be measured with other fractal dimensions, e.g. the divider method applied to range boundary lines (Gautestad and Myserud 1994) or the semivariance method for characterising the roughness of an abundance surface (Maurer and Heywood 1993).

For the Alaskan trees, we again used box-counting on all records, but this time applied eq. 4, i.e. we regressed the observed *proportion* of the maximum possible boxes occupied against scale, where the number of possible boxes is determined by the pattern of potentially occupiable sites in the study area: the fitted exponent is  $2-D$ . This ‘proportional’ estimation method is equivalent to correcting a species distribution  $D$  estimated using eq. 3 for the underlying  $D$  of the pattern of the sites in the study area (Mandelbrot 1977), such that  $D_{\text{obs}} = D_{\text{sites}} + D_{\text{true}} - 2$ , where  $D_{\text{obs}}$  is the measured dimension which is the outcome of the intersection of  $D_{\text{sites}}$ , the dimension associated with the particular distribution of study sites, and  $D_{\text{true}}$ , the true dimension of the underlying species distribution. This correction is unnecessary in the British grasses dataset, as the study area is rectangular and completely surveyed. For both the trees and the grasses  $n_0$  was allowed to vary away from unity, thus when calculating the expected SAR (eq. 5),  $p_i$  was constrained within the interval  $s^2 \leq p \leq 1$ .

## Results

### Alaskan trees

The log-log scaling plots used to estimate  $D$  are given for each of the eight tree species in Fig. 2. All species show a downward curvature (departure from linearity) in the observed proportion of quadrats occupied. Using the fitted parameters ( $D$  and  $n_0$  for each species) and eq. 5 to estimate the fractal SAR (Fig. 3) results in a SAR

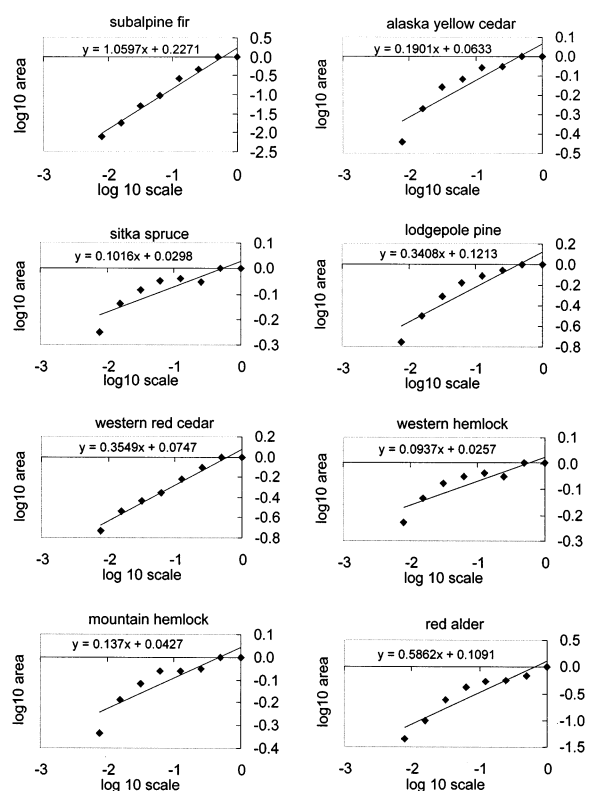


Fig. 2. Log-log scaling plots (scale-area curves) used to estimate the fractal dimension  $D$  for the eight Alaskan tree species. The exponent in the fitted power-law (regression coefficient of log scale) estimates  $2-D$  (eq. 4). Downward curvature in the relationship between the (log) proportion of occupiable sites and (log) scale is evident for most species. Common names translate, reading left to right from top, as: *Abies lasiocarpa* (Hook.) Nutt., *Chamaecyparis nootkatensis* (D. Don) Spach, *Picea sitchensis* (Bong.) Carr., *Pinus contorta* Dougl. var. *contorta*, *Thuja plicata* D. Don, *Tsuga heterophylla* (Raf.) Sarg., *Tsuga mertensiana* (Bong.) Carr. and *Alnus rubra* Bong.

with the characteristic upward curve at all but the coarsest scale (Fig. 1). The observed SAR of the SEAK forestry dataset, however, was either linear or somewhat decelerating at all scales, as is typical of many empirical SARs. The decreasing slope in the predicted SARs at very coarse scales is partly explained by all tree species distributions having estimated  $n_0 > 1$  (i.e.  $\log(n_0) > 0$  in Fig. 2); this results in the requirement to impose the condition that  $p \leq 1$ , which reduces the increase in predicted richness at these coarse scales (large areas).

### British grasses

The distribution of observed values of the fractal dimension  $D$  amongst British grasses was decidedly non-uniform; whilst there is a fairly even spread of  $D$  values from 0.4 to 1.6, there is an excess of species with high

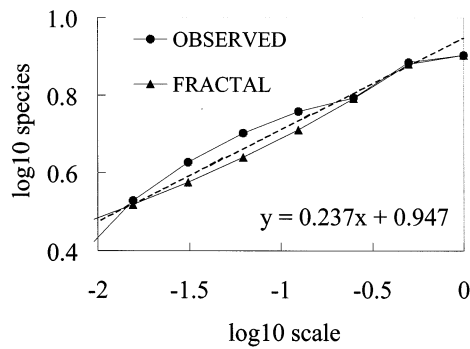


Fig. 3. Observed and fractal species-area relationships for the eight Alaskan tree species. The fractal SAR was estimated using eq. 5. The spatial structuring of the potentially occupiable sites was taken into account. There is an upward curvature of the expected number of species relative to both the empirically observed SAR and to a linear relationship expected from the power-law SAR. The regression fit of the observed species number vs scale for the power-law SAR is shown (dashed line); the exponent  $z$  of the power-law is 0.12 (the coefficient for area is half that for scale).

values of 1.6 or greater (Fig. 4). When these fractal  $D$ s and intercept parameters  $n_0$  are incorporated into a fractal SAR model using eq. 5, the pattern observed in the case of the Alaskan trees and in the theoretical case of uniformly distributed  $D$ s is found again: over-prediction at fine scales, and under-prediction at intermediate scales (Fig. 5). In contrast, the observed SAR shows a downward curvature at coarser scales compared to the linear relationship expected from a power-law SAR. This decelerating (approximately semi-logarithmic) relationship is not uncommon (Connor and McCoy 1979), but stands in marked contrast to the accelerating

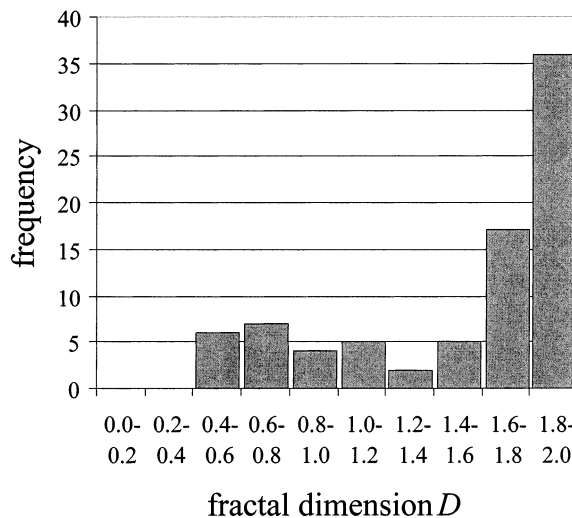


Fig. 4. Frequency distribution of estimated fractal dimensions of British grass spatial distributions. In the permissible range of zero to two, there is a clear trend for most species to have larger fractal dimensions.

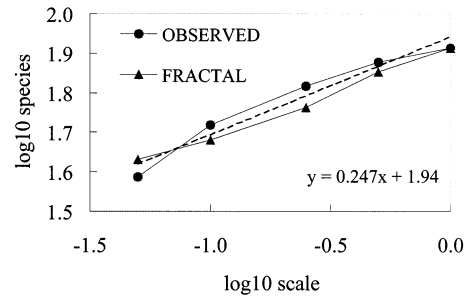


Fig. 5. Observed and fractal species-area relationships for the 82 British grass species. A  $\log_{10}$  (scale) of zero represents the whole study area of  $200 \times 200$  km, while a  $\log_{10}$  (scale) of  $-1.3$  indicates a single  $10 \times 10$  km quadrat. As was the case with the Alaskan trees (Fig. 3), this fractal SAR (eq. 5) is upwardly accelerating relative to both the observed data and the classic power-law linear relationship. The latter model fitted to the observed data is indicated by the dashed line. The estimated exponent  $z$  of the power-law SAR is half the coefficient of the  $x$ -variable (log scale) shown, almost identical to that of the power-law relationship for Alaskan trees (Fig. 3).

relationship predicted by summing dissimilar fractal species distributions.

## Discussion

Understanding SARs in theoretical terms using definitions of individual species' spatial structure is a growing theme in ecology. Such definitions have ranged from purely random (homogeneous Poisson) patterns of incidence, with identical species range limits across all species (Coleman 1981) to purely deterministic (present everywhere within range) but with stochastic range sizes (Leitner and Rosenzweig 1997), to more realistic, patchy distribution models (Ney-Nifle and Mangel 1999). The fractal SAR model we discuss here is conceptually closest to the two later approaches, since it includes aggregated spatial structure. However, the gains made by the relative simplicity of the fractal SAR model (two parameters per species and its inherent cross-scale properties) must be offset by the riskiness of assuming that species ranges are indeed fractal. We have presented some evidence here that, on the whole, they are not.

It is clear that the difference between the (variable  $D$ ) fractal SAR and the power-law SAR shows that interpreting empirical evidence *against* the power-law SAR as evidence that self-similarity has been broken is unfounded. Indeed, so long as species differ in fractal properties, the existence of a power-law SAR suggests departure from fractality, by at least some of the species involved. This conclusion might be disputed on the grounds that we have chosen an inappropriate distribution of  $D$ s for our analytical model: for example, it might be thought that the curvature of the fractal SAR (Fig. 1) on log-log axes depends on this particular case (uniform distribution of  $D$ s), but this is apparently not

so. We have tried a range of different permutations of  $D$ s across species, and the upward curvature was always found (Kunin and Lennon 2001). The only way in which truly fractal species distributions can combine to produce a log-log SAR that is not constantly accelerating is if all species have distributions with the same  $D$ , as modelled by Harte et al. (1999a, b). It is worth mentioning here that Maddux and Athreya (1999) have tried to show that Harte et al.'s model is actually only valid for particular values of  $a$  (and hence  $D$ ), but we agree with Harte et al. that this criticism is unfounded, relying as it does on strangely-shaped (e.g. L-shaped) sampling areas.

Since fractal species distributions do not combine to produce realistic SARs, what does this tell us about real species distributions? If one accepts that the power-law (or even the semi-log relationship) SAR is usually the best description of spatial scaling in real-world assemblages (see Rosenzweig 1995) – although this is not really a settled issue (Connor and McCoy 1979) – then it follows that all species cannot have fractal distributions. As a first point of departure we incorporated the logical constraints suggested by “quasi”-fractal distributions where the prefactor  $n_0$  may be greater or less than unity. This model produced a predicted SAR that accelerates at fine scales and then decelerates at coarse scales when plotted on logarithmic axes. Recent results, both theoretical and empirical, suggest that such a sigmoidal SAR may be more common than previously thought (Leitner and Rosenzweig 1997, Lomolino 2000, Plotkin et al. 2000, Crawley and Hurrall 2001), although a power-law is often an adequate first approximation.

Perhaps more realistic expectations for real-world species distributions are a mixture of the following: (i) some species in an assemblage may have self-similar distributions across a relatively wide range of scales, but other species may not, (ii) some species may have one fractal dimension across one range of scales but a different  $D$  across another range of scales, or have trends in  $D$  across scales, (iii) individual species may have distributions that are more self-similar in some parts of their geographical range than in others, and (iv) some species may have one  $D$  in some parts of its range (e.g. core areas) but a different  $D$  in other parts of its range (e.g. the margins). This list is obviously far from exhaustive, and a spectrum of the above cases is likely.

In the present study, we did not look for reasons (iii) and (iv), but we found that (i) and (ii) are probably true. Individual species distributions tended to be less dense at fine scales than expected from a fractal extrapolation of the number of occupied quadrats at coarser scales. In other words, there was a consistent trend for  $D$  to decrease with increasing spatial resolution. This is evident from the downward curve of proportion of quadrats occupied at finer scales in the Alaskan tree data (Fig. 2), and was also observed in the grass data.

Similar curvature in scale-area curves was noted by Kunin (1998) for scarce British plants and by He and Gaston (2000) for tropical forest trees, suggesting that such departures from linearity may be a common occurrence. Although random under-sampling at fine scales might produce this pattern, the quality of the Alaskan data in particular makes this unlikely. Currently there are no formal statistical tests designed to determine whether particular distributions deviate significantly from fractal scaling; partly this is due to a lack of appropriate alternative models that can be expressed in the same terms. Nonetheless, the apparent and repeated pattern of curvature in Fig. 2 certainly suggests a frequent departure from fractal scaling.

Are there any reasons, a priori, for thinking that species distributions should or should not be fractal? We know that some important abiotic constraints on species distributions are approximately fractal (e.g. topography, coastlines; Mandelbrot 1977) across some range of scales, while others (e.g. temperature, Lennon et al. 2000) are probably not. One possibility is that species' distributions are the outcome of a combination of factors including some physical constraints with fractal properties and others that are essentially random (white noise) processes operating at relatively fine scales only. In combination these constraints would produce convex scale-area curves for each individual species (as we observed), which combine to form approximately linear log-log SARs.

The logistic constraints of collecting biological data, and the limitations of the box-counting method of analysis may also lead to truly fractal distributions appearing non-fractal (or vice versa). Gautestad and Myrsterud (1994) describe two possible sampling biases: the first, which they term the “dilution effect”, occurs when sampling effort is inadequate and there are fewer recorded presences than there ought to be. This will depress the value of  $n$ , particularly at fine scales where boxes are more likely to be deemed ‘occupied’ on the strength of a single record, leading to a depression of the scale-area curve at fine scales. However, this assumes that recorder effort itself is evenly distributed (or at least homogeneous Poisson), when in reality it is likely that effort has an aggregated spatial structure, thus biases could be introduced at coarser scales too. If the spatial structure of recorder effort is known, then its effect on the observed scale-area curve can be accounted for (as was done with the Alaskan tree dataset in this paper). The converse of the inadequate sampling effort problem is the “time-fill” effect, where a distribution is studied over an extended time period and more and more records accumulate. Gautestad and Myrsterud argue that in such an instance, the distribution pattern will tend towards a solidly filled map,  $D = 2$ . But again the assumption of spatial independence is made, this time with new records occurring independently of the

old, whereas in reality new records will tend to be discovered (or produced through population growth and dispersal) near to old records, and the tendency towards  $D=2$  will be much weaker, if not absent entirely, as long as the distribution is not measured at too coarse a scale. Clearly the two problems are related and can be thought of as artifacts of the box-counting method caused by using too fine a grid (when data are sparse) or too coarse a grid (when data are abundant). This second case has also been called the “saturation effect” (Kunin et al. 2000). Despite these problems, box-counting is an intuitive and computational straight-forward method that has obvious connections with biological sampling techniques used in single-species and community studies. For a fuller discussion of its limitations, and alternative methods of estimating fractal dimensions, see Peitgen et al. (1992), Dubrulle and Lachiezerey (1994), Bérubé and Jébrak (1999), and Appendix 2.

In contrast with the large literature on the species-area relationship, the spatial scaling structure of individual species distributions has been relatively neglected. We suggest that one way forward for understanding how diversity scaling arises out of the spatial scaling structure of individual species distributions lies in, first, empirically finding the extent to which species fall into the fuzzy categories outlined earlier, and second, considering the consequences of these different kinds of departures from fractality for emergent SARs. Modelling and analysis of contrasting spatial patterns of incidence, and the way in which they combine, may eventually provide us with a much more secure basis for understanding the circumstances under which different SARs arise, as well as related emergent properties such as endemism and species turnover patterns.

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$$f(p) = -\frac{1}{2p \ln s}$$

This is the pdf of  $p$ . The expected value of  $p$  is the integral of  $p \cdot f(p)$  with limits given by the possible extreme values of  $p$  occurring at  $D = 0$  and  $D = 2$ :

$$E(p) = \int_1^{s^2} p \frac{1}{2p \ln s} dp = \left[ \frac{p}{2 \ln s} \right]_1^{s^2} = \frac{1 - s^2}{-2 \ln s}$$

This is the expected probability of presence in a quadrat of area  $s^2$  of a single species chosen to have a fractal  $D$  between 0 and 2 with equal likelihood. Since all species are independent, if there are  $R_{max}$  species, then the fractal species SAR is:

$$E(R) = \frac{R_{max}(1 - A)}{-\ln A}$$

where  $E(R)$  is expected species richness,  $A$  is area and  $R_{max}$  is the number of species present in the entire study area. As  $A \rightarrow 1$ ,  $E(R) \rightarrow R_{max}$ .

## Appendix 1

### Derivation of fractal SAR

To derive the SAR for fractally-distributed species where species have different fractal dimensions  $D$ , we applied standard methods for deriving the probability density function (pdf) of a function of a random variable (Wackerly et al. 1996). In our case, the random variable is  $D$ , and we define it as having a uniform distribution between 0 and 2:

$$g(D) = 1/2; \quad 0 < D < 2$$

where  $g(D)$  is the pdf of the random variable  $D$ . Our function of this random variable is that which gives the probability of presence of a species with a given  $D$  in a particular size of quadrat, eq. 4, but with the prefactor  $n_0$  set to unity:

$$p = s^{2-D}$$

Our initial goal is finding the probability density function of the distribution of  $p$  values across species given the uniform distribution of  $D$  across species. The “method of transformations” defines this density function such that:

$$f(p) = g(D) \frac{\partial D(p)}{\partial p}$$

where  $D(p)$  is the inverse function of eq. 4, expressing  $D$  as a function of  $p$ :

$$D(p) = 2 - \frac{\ln p}{\ln s}$$

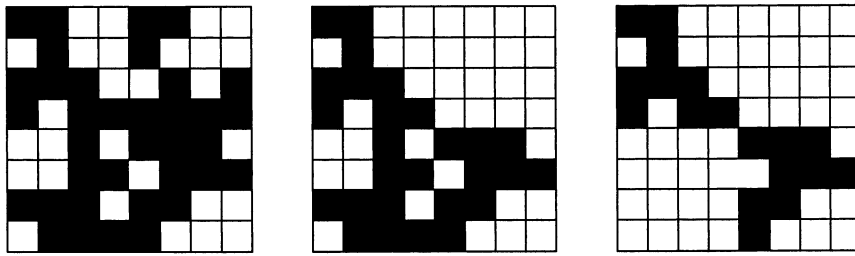
Thus,

## Appendix 2

### Fractals and quasi-fractals

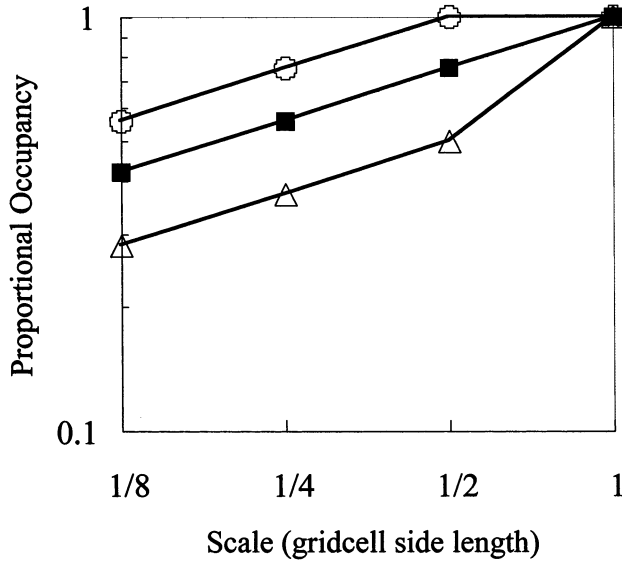
Consider the box-counting method of measuring the fractal dimension of an object. In this case the object of interest is a species’ distribution pattern, viewed as a set of occupied and unoccupied grid cells. If the species is present at all, then all such patterns must have a proportional occupancy of  $p = 1$  when measured at the coarsest possible scale of  $s = 1$  (i.e. a grid with one single large cell equal to the extent of the study area). Fractal distributions are recognised by the fact that they produce a straight-line plot of  $\log(\text{occupancy})$  vs  $\log(\text{scale})$ , where the fractal dimension,  $D$ , is a simple function of the slope. In the case of a true mathematical fractal this relationship is assumed to hold over all ranges of scale,  $0 \leq s \leq 1$ . Given that the line must pass through the point  $s = 1$  and  $p = 1$ , this means that, for an “ideal” fractal, proportional occupancy as a function of scale is uniquely defined by  $D$ , since  $n_0$  (the value of  $p$  when  $s = 1$ , eq. 4) is implicitly constrained to equal one.

Real-world objects (e.g. species distributions) can often be considered as “quasi-fractals” when they display self-similarity over a large, but finite range of scales (Stewart 2000). Applying the box-counting method to such objects will result in a straight line plot between some minimum and maximum range of scales,  $s_{min} \leq s \leq s_{max}$ , but an extrapolation of this portion of the line will not necessarily pass through the point (1,1) – see Fig. A1. Therefore, the description of a quasi-



(a)  $D'=1.59, n_0 = 1.33; D = 1.71$     (b)  $D'=1.59, n_0 = 1; D = 1.59$     (c)  $D'=1.59, n_0 = 0.66; D = 1.41$

Fig. A1. Three artificial species distributions (top) and their corresponding scale-area curves (bottom): (a) a “dense” quasi-fractal, open circles, (b) an “ideal” fractal, solid squares, (c) a “sparse” quasi-fractal, open triangles.  $D'$  and  $n_0$  were calculated by regression of  $\log(\text{occupancy})$  vs  $\log(\text{scale})$  for  $\frac{1}{8} \leq s \leq \frac{1}{2}$  (eqn. 2).  $D$  was calculated by regression of  $\log(\text{occupancy})$  vs  $\log(\text{scale})$  for  $\frac{1}{8} \leq s \leq 1$ , forcing the relationship through the point ( $s = 1, p = 1$ ), i.e. setting  $n_0 = 1$ .



fractal is achieved by letting  $n_0$  vary away from unity, with the implicit recognition that the fractal dimension  $D$  is unlikely to hold for all scales. Many practical methods for measuring  $D$  recommend that  $s_{\max} \leq 0.5$  or

$s_{\max} \leq$  the relative radius of the object under study (Allain and Cloitre 1991, Pfeifer and Obert 1989), since above these scales there is too little information to make an accurate determination of  $D$ .