**Opinion** is intended to facilitate communication between reader and author and reader and reader. Comments, viewpoints or suggestions arising from published papers are welcome. Discussion and debate about important issues in ecology, e.g. theory or terminology, may also be included. Contributions should be as precise as possible and references should be kept to a minimum. A summary is not required.

# *A community-level fractal property produces power-law species-area relationships*

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Power-law relationships appear to characterize many patterns observed in ecology, from the level of individuals to the level of ecosystems (Calder 1984, Gaston and Blackburn 2000). These power laws often hold over scale ranges sufficiently large to justify the search for a unifying theoretical framework explaining the relationship between these patterns. A promising avenue for discovering such a framework is the exploration of the fractal properties from which these power laws derive and their implications for other ecological characteristics. In this vein, Harte and Kinzig (1997) and Harte et al. (1999a) studied the fractal property behind a power-law species-area relationship and its implications for other species distribution characteristics.

In a recent paper published in Oikos, Lennon et al. (2002) claim that in order to derive a power-law species-area relationship from fractals in the distribution of species, Harte et al. (1999a) assumed that individual species distributions are fractal and that all species patterns have the same fractal dimension D. Inspired by empirical evidence that indicates that fractal dimension tends to vary between species, they then show that in this more realistic case of varying D, the species-area relationship does not follow a power law. Hence Lennon et al. (2002) conclude that, despite Harte et al. (1999a) derivation of the power-law species-area relationship from fractals, a fractal distribution of species is not what produces power-law species-area relationships in nature.

We show here the misleading error in Lennon et al.'s (2002) critique. Harte et al. (1999a) did not derive the power-law species-area relationship from fractals at the 'species-level', but rather from a 'community-level' fractal property that can hold without the presence of 'species-level' fractals. Furthermore, this community-level fractal property holds in any region where the power-law species-area relationship holds (Harte and Kinzig 1997). Hence this community-level fractal property must be what produces power-law species-area relationships in nature – it is equivalent to it. Lennon et al. are correct that if the species-level fractal property holds for each species in a community, a power-law species-area relationship will result only if the fractal dimension is constant across species. This result was found previously in Harte et al. (2001), where the overall degree of compatibility between the community-level and species-level fractal properties was derived. However, as Harte et al. (2001) showed, the community-level fractal property and hence the power-law species-area relationship can exist either if the fractal dimension is constant across species, or if some individual species distributions are not fractal on their own. This does not rule out the possibility that species-level fractals are important in nature. Below we provide a detailed analysis of these issues.

## Equivalence of a community-level fractal and the power-law species-area relationship

A fractal is a geometric object that is self-similar, meaning it can be thought of as a set of consistently rescaled copies of itself (Addison 1997). Most fractals in nature are "statistical" and "finite", meaning that they are not made up of exact copies of themselves, but rather their average properties are self-similar over some finite scale range. Fractal objects are described as 'scale-invariant' in the sense that they look the same when one "zooms in" or "zooms out" on them, i.e. when one looks at them on a smaller or larger scale.

Scale invariance is the fundamental property behind all power laws, meaning relationships of the form $Y \propto M^b$. In particular, if a doubling of M leads to a Y that is $2^b$ times as large, no matter what value, or scale, of M you start with, the relationship between Y and M will follow the power law $Y \propto M^b$. Hence there is an intimate relationship between power laws and fractals. Power laws observed in nature can often be equated to self-similarity properties (also called "fractal" properties) that are useful for understanding the power law's causes and connections with other observed phenomena.

By building on work in Harte and Kinzig (1997), Harte et al. (1999a) showed that the often observed power-law relationship between the mean number of species present in a patch, S, and the area of that patch, A, written as $S = cA^z$, can be equated to a fractal property of the distribution of species. In particular, it can be equated to a community-level fractal property that is different from the species-level fractal property discussed by Lennon et al. (2002). The species-level fractal property is instead equivalent to a power-law relationship between the box-counting measurement of a species' range R, and the area of the box used to measure it, A, written as $R = CA^{y'}$ (Harte et al. 2001). In this section, we define the community-level fractal property and provide a more detailed version of the Harte and Kinzig (1997) as well as the Harte et al. (1999a) proof of its equivalence to the power-law species-area relationship. Hence we provide a detailed explanation of why Lennon et al. were incorrect in concluding that a fractal distribution of species is not what produces power-law species-area relationships in nature.

First we define the community-level fractal property. Consider a region of contiguous habitat of area $A_0$, and the set of species within a broadly defined taxonomic group, or "community", such as 'birds' or 'plants'. Let $A_i = A_0/2^i$ be the area of patches that are obtained from the region $A_0$ through i bi-sections. Consider a patch randomly chosen from those of size $A_{i-1}$ that are located within $A_0$, and a species randomly chosen from the list of species that are present in that patch. We assume that nothing else about that species (such as its abundance) is known, and define $a_i$ to be the probability that this species is also present in a particular one of the two patches of area $A_i$ contained in the chosen $A_{i-1}$-sized patch. The distribution of species is fractal at the community-level if $a_i$ is independent of i, i.e. if $a_i = a$ for all i. We refer to $a_i$ as the "community-level self-similarity parameter". This condition makes the distribution of species a fractal because it means that "species occurrences" are on average distributed the same way at small and large scales and hence that the distribution of species is, on average, self-similar. By a "species occurrence" at the $i-1$ scale, we simply mean an instance of a species being present in a patch of area $A_{i-1}$.

Note that the community-level self-similarity probability $a_i$ is applicable to a species occurrence at the $i-1$ scale that is drawn at random from all such species occurrences within $A_0$. If there are $2^{i-1}$ patches of size $A_{i-1}$ in $A_0$, there will be $2^{i-1} \times S_{i-1}$ species occurrences at the $i-1$ scale in $A_0$, where $S_{i-1}$ is the mean species richness in patches of size $A_{i-1}$ within $A_0$. The probability $a_i$ may or may not accurately describe non-randomly selected sub-sets of these $2^{i-1} \times S_{i-1}$ species occurrences, such as all of the occurrences of just one particular species.

We now explain how to measure the probability $a_i$ from species distribution data, a concept that will be the key to demonstrating the equivalence of this community-level fractal property and the power-law species-area relationship. Recall from probability theory that the probability of an event is measured as follows:

$$\text{the probability of an event} = \frac{\text{the number of trials for which the event happens}}{\text{the total number of trials}} \quad (1)$$

In measuring the community-level self-similarity parameter $a_i$, there are two trials for every species occurrence at the $i-1$ scale (one for each $A_i$ within the $A_{i-1}$ where the presence occurs). Hence in a region of area $A_0$, the total number of trials is equal to $2 \times 2^{i-1} \times S_{i-1}$, where, as mentioned above, $2^{i-1} \times S_{i-1}$ is the number of species occurrences at the $i-1$ scale. The event whose probability we are measuring happens for every species occurrence at the *i* scale. Hence the number of trials for which the event happens is $2^{i-1} \times S_i$. Following Eq. (1), $a_i$ can therefore be estimated from species distribution data as

$$a_i = \frac{2^i \times S_i}{2 \times 2^{i-1} \times S_{i-1}} = \frac{S_i}{S_{i-1}} \quad (2)$$

i.e. it is the ratio of the mean species richness at the i spatial scale to the mean species richness at the $i-1$ scale. We call the distribution of species fractal at the community-level if this measured ratio is approximately constant with scale i.

We now show that the community-level fractal property we've defined is equivalent to the power-law species-area relationship, i.e. that the existence of the fractal property implies that the power-law species-area relationship holds, and that the converse is also true. We begin by assuming that the power-law species-area relationship holds within a region of area $A_0$. Given this assumption, the mean species richness of a broad taxonomic grouping, $S_i$, across all patches of size $A_i$ within $A_0$ is given by

$$S_i = cA_i^z \quad (3)$$

where c and z are constants that may vary across taxonomic groupings (Rosenzweig 1995). We can now measure $a_i$ at each scale i, and determine if it will be constant with i in this situation. Substituting this expression for the mean species richness into Eq. (2), we obtain

$$a_i = \frac{cA_i^z}{cA_{i-1}^z} = \left(\frac{A_0/2^i}{A_0/2^{i-1}}\right)^z = 2^{-z} \quad (4)$$

Eq. (4) says that for all i, $a_i = a$, where $a \equiv 2^{-z}$defines a. It says that $a_i$ is independent of i for a region in which the power-law species-area relationship holds. Hence the community-level fractal property holds within a region given that the power-law species-area relationship holds within it.

Now, in order to prove the converse, we instead assume that the community-level fractal property holds within a region of area $A_0$. That is, we assume that $a_i = a$ for all i, where $a_i$ is the community-level self-similarity parameter and a is simply some constant that we will later relate to z. We return again to Eq. (2). By inverting this equation and using the community-level fractal property, we find that $S_i = aS_{i-1}$ for all i, and hence

$$S_i = a^i S_0 \quad (5)$$

We can write $a^i$ in terms of the patch size $A_i$ as follows

$$a^i = 2^{i\cdot\log_2(a)} = (2^{-i})^{-\log_2(a)} = \left(\frac{A_i}{A_0}\right)^{-\log_2(a)} \quad (6)$$

Plugging Eq. (6) into Eq. (5), we obtain

$$S_i = S_0\left(\frac{A_i}{A_0}\right)^{-\log_2(a)} \quad (7)$$

which is just a power-law species-area relationship like that in Eq. (3), with $z = -\log_2(a)$ and $c = S_0/(A_0)^z$. Hence the power-law species-area relationship holds within a region given that the community-level fractal property holds within it, and we have shown that these two properties are equivalent. A community-level fractal must be what produces power-law species-area relationships in nature, because it is mathematically equivalent to the power-law.

## The degree of compatibility of community and species-level fractals

In this section we provide a more detailed and general version of the Harte et al. (2001) derivation of the degree of compatibility of community and species-level fractals. We begin by defining the species-level fractal property and describing how the species-level version of the self-similarity parameter is measured.

The species-level fractal property considered by Lennon et al. (2002) and Harte et al. (2001) is defined in an analogous way to the community-level fractal property, but has to do with the distribution of each particular species, rather than a species chosen at random from those present in a given patch. Once again consider a region of area $A_0$ and the patches of area $A_i = A_0/2^i$ that are obtained from $A_0$ upon i bi-sections. For species-level self-similarity, at every spatial scale i there is a set of probabilities $\{\alpha_i\}$, where each member of the set characterizes the statistical properties of the spatial distribution of a particular species as follows. For a particular species, let $\alpha_i$ be the probability that if it is found in a randomly chosen patch of area $A_{i-1}$, then it is found in a particular one of the two patches of area $A_i$ contained in the chosen $A_{i-1}$-sized patch. The distribution of a species is self-similar, or fractal, at the species-level if the $\alpha_i$ for that species is independent of i, i.e. if $\alpha_i = \alpha$ for all i. Note that the constants $\alpha_i$ can differ from species to species, and that species-level self-similarity may hold for some species within a community but not others. For each species, we refer to its $\alpha_i$ as its "species-level self-similarity parameter".

In measuring the species-level self-similarity parameter $\alpha_i$ for a particular species, there are two trials for every instance of a presence of that species in a patch of area $A_i$ (one for each $A_{i-1}$ within that $A_i$). Hence in a patch of size $A_0$, the total number of trials is equal to $2 \times W_{i-1}$, where $W_{i-1}$ is the number of patches of size $A_{i-1}$ within $A_0$ that the species is present in. The event happens for every instance of a presence of the species in a patch of size $A_i$, and hence the number of trials for which the event happens is simply $W_i$. Following Eq. (1), $\alpha_i$ can be estimated from species distribution data as

$$\alpha_i = \frac{W_i}{2 \times W_{i-1}} = \frac{(R_i/A_i)}{2 \times (R_{i-1}/A_{i-1})} = \frac{R_i}{R_{i-1}} \quad (8)$$

where $R_i$ is the box-counting measurement of a species-range, which we'll subsequently refer to simply as the "range size", made using a box of area $A_i$. By definition $R_i$ is equal to $W_i \times A_i$. We call the distribution of the species in question fractal if the measured ratio of a species' range size at adjacent scales i and $i-1$ is approximately constant with scale i. Using Eq. (8) and a sequence of steps analogous to those in the proof in the previous section, one can show (Harte et al. 2001) that the species-level fractal property is equivalent to the power-law relationship between a species' range size, and the area of the box used to measure it, i.e. a "range-area" relationship of the form

$$R_i = CA_i^{y'} \quad (9)$$

where y′ is a constant that can vary across species and $\alpha = 2^{-y'}$. As Lennon et al. (2002) explained, the self-similarity parameter $\alpha$ can be related to the box-counting measure of the fractal dimension D of the species by $D = 2(1 + \log_2(\alpha))$.

Paralleling Harte et al. (2001), we now derive a general relationship between the community-level self-similarity parameter $a_i$ and the species-level self-similarity parameters $\{\alpha_i\}$, and from it infer the degree of compatibility of the community-level fractal and species-level fractals. We will need the following expression for the mean species richness at scale i, $S_i$, in terms of the box-counting measure of range for each of the species at scale i, the $\{R_i\}$:

$$S_i = \frac{\sum_p (\#\ \text{of species in } A_{i,p})}{2^i}$$

$$= \frac{\sum_k (\#\ \text{of } A_i \text{ species k is in})}{2^i} = \frac{\sum_k W_{i,k}}{2^i} = \frac{\sum_k R_{i,k}}{A_0}$$

$$= \frac{\langle R_i \rangle}{S_0 A_0} \tag{10}$$

In Eq. (10), p labels the $2^i$ different patches of area $A_i$ within $A_0$, k labels the $S_0$ species that are present in $A_0$, and $\langle\rangle$ indicates an average over those $S_0$ species. The first equality in Eq. (10) is simply from the definition of the mean species richness. The second equality results from transforming the sum across the $A_i$ of the number of species in each $A_i$ into a sum over species of the number of $A_i$ each species is present in. The third and fourth equalities result from applying the definitions of $W_i$ and $R_i$ from above for each species k. Plugging the last expression for the mean species richness in Eq. (10) into Eq. (2), we obtain the following expression for the community-level self-similarity parameter.

$$a_i = \frac{\langle R_i \rangle}{\langle R_{i-1} \rangle} \tag{11}$$

In words, the parameter $a_i$ can be obtained from the ratio of the range size measured at scale i and averaged across the species to that measured at scale $i-1$. We can convert Eq. (11) into a relationship between $a_i$ and the $\{\alpha_i\}$ by writing the $R_i$ for each species in terms of its $\alpha_i$. Solving Eq. (8) for $R_i$ we have $R_i = \alpha_i R_{i-1}$. Applying this expression repeatedly from scale $j = 0$ to scale $j = i$,

$$R_i = \left( \prod_{j=1}^{i} \alpha_j \right) R_0 \tag{12}$$

By substituting Eq. (12) into Eq. (11), we obtain

$$a_i = \frac{\left\langle \prod_{j=1}^{i} \alpha_j \right\rangle}{\left\langle \prod_{j=1}^{i-1} \alpha_j \right\rangle} \tag{13}$$

where again $\langle\rangle$ indicates an average over the $S_0$ species present in $A_0$. This relationship between $a_i$ and the $\{\alpha_i\}$ was previously derived by Harte et al. (2001) using the assumption that species are distributed independently of one another and the assumption that the distribution of a species within one $A_i$ of an $A_{i-1}$ is independent of its distribution within the other $A_i$. The derivation here makes no such assumptions and hence shows that the relationship in Eq. (13) applies in general.

As originally found in Harte et al. (2001), Eq. (13) implies that a can be scale independent, or equivalently the power-law form of the species-area relationship can hold, if either 1) all of the $\alpha$'s are scale independent and equal to a, or 2) there is 'enough' scale dependence in the $\alpha_i$ of one or more species. In the latter mode, $\alpha$ can vary across the species for which it is scale-invariant. Scale-independent $\alpha$'s cause a to increase with i, at a rate that depends on the distribution of the $\alpha$ across species. By 'enough' scale dependence in the $\alpha_i$ of one or more of the species, we simply mean enough to counteract this increase to give a constant a over the scale range for which the power-law species-area relationship holds. How many species are required to have scale-dependent $\alpha_i$ depends on how much $\alpha$ varies across species with fractal distributions, and the range of scales over which a must be constant. Table 1 shows how scale independence of a can arise through this second mode, scale dependence at the species level, in some simple, three-species cases. In these cases, scale dependence in just one of the three species distributions is enough to yield a scale-independent a, but the range of scales for which it can yield community-level scale-invariance depends on how much $\alpha$ differs between the two fractal species.

To summarize, Harte et al. (2001) showed that the community-level fractal property can hold only if either 1) the species-level fractal property holds for each species with the same fractal dimension D, or 2) there is 'enough' divergence from the species-level fractal property of one or more of the species distributions. In the latter case, the fractal dimension can vary across those species that do exhibit the species-level fractal property without the community-level fractal property being broken. Lennon et al. are correct that if each species distribution is fractal but the fractal dimension D varies between species, the species-area relationship will not be a power law (Harte et al. 2001 already showed this). However, by ignoring the possibility of a 'community-level' fractal that could arise in the absence, or partial absence, of species-level fractals, they incorrectly concluded from this result that fractals in the distribution of species are not what produce power-law species-area relationships in nature. Furthermore, Harte et al.'s, and

Table 1. This table shows a set of three-species cases for which scale invariance in one of the three species distributions is enough to give a scale-independent a. The scale i to which $a_i$ is constant with respect to i increases as the difference between the $\alpha$ of species 1 and the $\alpha$ of species 2 decreases. Species 3's $\alpha_i$ were obtained iteratively at each scale i according to $\alpha_i = (S_0 a^i - (S_0 - 1)\langle \alpha^i \rangle) / \prod_{j=1}^{i-1} \alpha_j$, where the $\langle\rangle$ indicate an average over all of the other, fractally distributed, species. This expression can be shown to follow from Eq. (13) if just one species exhibits scale dependence. The scale i to which $a_i$ can be made equal to the constant value of $a = 0.75$ by scale dependence in the distribution of species 3 is the largest i for which species 3's $\alpha_i$ is greater than 0.5, the lower bound of any $\alpha$.

| $a = 0.75$ | Case 1 | Case 2 | Case 3 | Case 4 | Case 5 |
|---|---|---|---|---|---|
| Species 1's $\alpha$ | 1.00 | 0.95 | 0.90 | 0.85 | 0.80 |
| Species 2's $\alpha$ | 0.50 | 0.55 | 0.60 | 0.65 | 0.70 |
| Scale i to which $a_i = a$ | 2 | 3 | 4 | 6 | 13 |
| Species 3's $\alpha_i$ | | | | | |
| $i = 1$ | 0.75 | 0.75 | 0.75 | 0.75 | 0.75 |
| 2 | 0.58 | 0.64 | 0.69 | 0.72 | 0.74 |
| 3 | | 0.50 | 0.62 | 0.69 | 0.73 |
| 4 | | | 0.51 | 0.66 | 0.73 |
| 5 | | | | 0.61 | 0.72 |
| 6 | | | | 0.53 | 0.71 |
| 7 | | | | | 0.70 |
| 8 | | | | | 0.67 |
| 9 | | | | | 0.68 |
| 10 | | | | | 0.66 |
| 11 | | | | | 0.63 |
| 12 | | | | | 0.52 |
| 13 | | | | | 0.52 |

Lennon et al.'s analyses do not rule out the possibility that species-level fractals are important in nature. How prevalent species-level fractals can be in principle is determined by how much the fractal dimension varies across species, and by the width of the scale range for which the power-law species-area relationship holds.

## Discussion

Lennon et al. (2002) claimed that, in order to derive the power-law species-area relationship from fractals in the distribution of species, Harte et al. (1999a) had to assume that the distribution of each species is fractal with the same fractal dimension D. This claim is incorrect; Harte et al. (1999a) used a broader 'community-level' fractal property to derive the power-law species-area relationship. Furthermore, this community-level fractal property must be relevant to power-law species-area relationships observed in nature, since it must hold in any region where the power-law species-area relationship holds. Hence ecologists can continue to turn to fractals in the distribution of species as a viable theoretical link between power-law species-area relationships and other power-law phenomena in ecology.

Note that we do not claim that this community-level fractal property is equivalent to the form for characteristics other than the species-area relationship predicted in Harte and Kinzig (1997) and in Harte et al. (1999a). In particular, the Harte and Kinzig (1997) prediction for the endemics-area relationship, and the Harte et al. (1999a) prediction for the species-abundance distribution do not follow from community-level self-similarity alone, but rather require the extension of the community-level self-similarity parameter a to particular non-randomly selected sub-sets of species occurrences, which, as mentioned in the first section, it may or may not describe.

Lennon et al. (2002) re-derived Harte et al.'s (2001) result that power-law species-area relationships do not result from species-level fractals if the fractal dimension varies across species. Lennon et al.'s (2002) analysis of data for Alaskan trees and British grasses indicates that fractal dimension tends to vary between species. Although the combination of this empirical evidence, and Lennon et al.'s (2002, or Harte et al. 2001) theoretical result, tell us that the species-level fractal property does not hold for all species in regions that exhibit the power-law species-area relationship, it does not rule out the possibility that species-level fractals are important in nature. Species-level fractals, in addition to the community-level fractal, may still be useful for making links with other power-law phenomena in ecology. Lennon et al. find in their own analyses, and point out in the literature, empirical evidence of a consistent decrease in fractal dimension with increasing spatial resolution, which may indicate departure from species-level fractals. Yet, as Lennon et al. point out, they and others have not been able to use this evidence to statistically reject the species-level fractal property (due to complexities of statistical analysis on nested data), and overall there has been little empirical study of the scaling of species-level distributions. Furthermore, the fractal model has performed well in some cases at predicting abundance (Kunin 1998, Finlayson 1999). Clearly, in

order to create a truly useful unifying theory of ecological power-law phenomena based on the community- and/or species-level fractal properties, ecologists need to come to a better empirical understanding of when (i.e. in what biological circumstances and over what scale ranges) these fractal properties hold, and when they don't.

A few further notes will be useful for the reader's deeper understanding of the equivalence between power-laws and fractal properties discussed in this paper. First, note that ecologists have studied two broad types of species-area relationships (Rosenzweig 1995): 1) those for patches that are part of a region of contiguous habitat, often called "mainland" species-area relationships; and 2) those for patches which are biologically isolated, often called "island" species-area relationships. The causes and consequences of these two types of species-area relationships may differ. We have shown the equivalence of a community-level fractal property with the power-law form of the first of these two types of species-area relationships, mainland species-area relationships. This community-level fractal property has implications for island species-area relationships, but equivalence with its power-law form does not hold. In particular, if the community-level fractal property defined above holds with the same parameter a within all of the isolate patches making up an island species-area curve, and if the species richness at the small scale where the fractal property breaks down is the same across isolates, the power-law nature of island species-area curve follows. However, the existence of a power-law island species-area curve does not imply that community-level self-similarity must hold within the isolate patches.

Second, note that empirical studies suggest that the relationship between species richness and area has shape dependence (Kunin 1997, Harte et al. 1999b). Hence in order to avoid the confounding effects of shape, one must examine the relationship between species richness and area for a set of patches that are all of the same shape. In defining the fractal properties of species distributions, we therefore mean for the patches $A_i$ to be similarly shaped. Exact shape preservation at every scale under bisection is achieved only if the region $A_0$ has a length-to-width ration of $\sqrt{2}$, so that repetitive bi-sections perpendicular to the long dimension yield at each stage rectangles that are identical in shape to $A_0$. However, for the purposes of showing the equivalence of community-level self-similarity and the power-law species-area relationship, or of species-level self-similarity and the power-law range-area relationship, there is nothing special about using bi-sections to get to smaller sized patches, and hence nothing special about the shape $1 \times \sqrt{2}$. Tri-sections, quadra-sections, etc. would work equally as well in the proof. Furthermore, one could outline the same proof for the case where the set of patches chosen at smaller scales do not completely cover the larger scale patches. In summary, the equivalence of the fractal properties and power-laws discussed in this paper can be shown for patches of any shape, as long as shape is preserved across the patches.

Third, one might try to argue that we have shown that the community-level fractal property leads to a power-law species-area relationship for patches of size $A_i$, but not necessarily power-law dependence for patches of the same shape but sized between some $A_i$ and some $A_{i-1}$ (i.e. patches of size $A'$, where $A_i < A' < A_{i-1}$). Two arguments indicate greater generality. First and more simply, if the community-level self-similarity property holds within a region of size $A_0$, it seems likely that it will also hold, with the same parameter a, in a slightly smaller region, $A_0'$, sized such that patches of size $A'$ can be obtained from it by bi-sections, or tri-sections, or some other division consistent with the division of $A_0$. Second, the degree to which the mean number of species in patches of size $A'$, $S(A')$, can vary from the power law when $S_i = cA_i^z$ holds is constrained to be small by the fact that mean species richness must monotonically increase with area for nested areas. Similar arguments could be made at the species-level.

Last, in calling the distribution of species "fractal" if the self-similarity parameter is constant with scale, we have used a broad definition of a fractal, namely that a fractal is an object which is self-similar. According to Addison (1997), Mandelbrot used this definition to replace a stricter definition that he initially proposed but later retracted. This stricter definition is that a fractal is an object whose fractal dimension is larger than its topological dimension. In simple terms, the topological dimension is the integer dimension one intuitively assigns to objects – 0 for a set of points, 1 for a line, 2 for a square, etc. The existence of a power-law species-area relationship also implies that the distribution of species is fractal in this stricter sense. Hastings and Sugihara (1993) showed that the fractal dimension of the set of points marking the location at which new species are discovered as one moves radially outward is 2z if the power-law species-area relationship holds. This is larger than the topological dimension of this object, which is 0 because it is simply a set of points. Similarly, the fractal dimension of the set of points representing the spatial location of the individuals of a single species is $2(1-y')$ if the power-law range-area relationship holds, where $y'$ is the range-area exponent in Eq. (9). This fractal dimension is also greater than the distribution's topological dimension of 0, and hence the species-level distribution satisfies this more stringent definition of fractal if the power-law range-area relationship holds. These are primarily mathematical fine points, however. The property we think is more useful for thinking intuitively about the spatial distribution of species, and for deriving the expected form of other characteristics of this distribution, is not the fractal dimension, but rather the scale-invariance of the self-similarity parameters a and $\alpha$.

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## References

Addison, P. S. 1997. Fractals and chaos. – Institute of Physics Publishing.

Calder, W. A. 1984. Size, function and life history. – Harvard Univ. Press.

Finlayson, J. C. 1999. Species abundance across spatial scales. – Science 283: 1979.

Gaston, K. and Blackburn, T. 2000. Macroecology. – Blackwell Science.

Harte, J. and Kinzig, A. P. 1997. On the implications of species-area relationships for endemism, spatial turnover, and food web patterns. – Oikos 80: 417–427.

Harte, J., Kinzig, A. P. and Green, J. 1999a. Self-similarity in the distribution and abundance of species. – Science 286: 334–336.

Harte, J., Mc Carthy, S., Taylor, K. et al. 1999b. Estimating species-area relationships from plot to landscape scale using spatial-turnover data. – Oikos 86: 45–54.

Harte, J., Blackburn, T. and Ostling, A. 2001. Self-similarity and the relationship between abundance and range size. – Am. Nat. 157: 374–386.

Hastings, H. and Sugihara, G. 1993. Fractals: a user's guide for the natural sciences. – Oxford Univ. Press.

Kunin, W. E. 1997. Sample shape, spatial scale and species counts: implications for reserve design. – Biol. Conserv. 82: 369–377.

Kunin, W. E. 1998. Extrapolating species abundance across spatial scales. – Science 281: 1513–1515.

Lennon, J. L., Kunin, W. E. and Hartley, S. 2002. Fractal species distributions do not produce power-law species-area relationships. – Oikos 97: 378–386.

Rosenzweig, M. L. 1995. Species diversity in space and time. – Cambridge Univ. Press.