

Self-Similarity, the Power Law Form of the Species-Area Relationship, and a Probability Rule: A Reply to Maddux

Annette Ostling,^{1,*} John Harte,^{1,†} Jessica L. Green,^{2,‡} and Ann P. Kinzig^{3,§}

1. Energy and Resources Group, University of California, Berkeley, California 94720-3050;

2. Department of Environmental Science and Policy, University of California, Davis, California 95616;

3. Department of Biology, Arizona State University, Tempe, Arizona 85287

Submitted May 20, 2003; Accepted December 18, 2003;
Electronically published XX

Keywords: species-area relationship, self-similarity, fractal, power law, scaling.

We reply here to the comment by Maddux (2004, in this issue), which discusses a fractal probability rule (PR) for the spatial distribution of species proposed by Harte and Kinzig (1997) and Harte et al. (1999b) as a means of deriving the characteristics of species distributions that exhibit power law species-area relationships. In his comment, Maddux derives certain properties of spatial distributions that follow this PR, including the dependence of the species richness in a patch on the location of that patch, and argues that these properties are biologically unlikely. He also argues that the PR leads to a power law relationship between species richness and area only for a discrete set of patch sizes and that it does not constrain the species-area relationship for areas that fall between these discrete sizes. On the basis of these arguments, Maddux concludes that the PR is not an adequate method for relating the power law species-area relationship (PLSAR) to an underlying fractal or self-similarity condition.

We agree with Maddux that the PR leads to distributions with unrealistic properties when it is used to simulate landscapes and that the PR leads to a discrete, rather than

continuous, power law species-area relationship. However, we do not think all of the properties Maddux points out are unrealistic. Furthermore, we believe that the PR could still provide a useful model for species distributions that exhibit power law species-area relationships if it is supplemented with instructions that enable the user to avoid unrealistic predictions. More importantly, although the fractal PR has failings, this PR is just one way of realizing a spatial distribution of species for which a more general, community-level fractal property (CFP) holds. This CFP is mathematically equivalent to the power law species-area relationship (Ostling et al. 2003), and, as we show for the first time here, this equivalence holds for a continuous set of patch sizes. Moreover, the CFP pinpoints exactly what about the spatial distribution of species is scale invariant if the power law species-area relationship holds, and hence it may provide insights into the mechanisms leading to power law species-area relationships and into how seemingly disparate power law phenomena in ecology might be related. We provide an in-depth discussion of these issues.

Unrealistic Consequences of the Probability Rule

We begin by describing the probability rule (PR) and showing how the biogeographic patterns Maddux dubbed as unrealistic follow from it. Consider a region of contiguous habitat of area A_0 containing S_0 species within some taxonomic group. Let $A_i = A_0/2^i$ be the area of equally sized and shaped cells that are obtained from A_0 through i bisections. By assuming that A_0 is a $2^{1/2} \times 1$ rectangle and that each bisection line is perpendicular to the long dimension of the rectangles at every scale, the bisection procedure is shape preserving. Let S_i be the average number of species in the 2^i patches of area A_i . The PR is as follows: given that a species is present in an A_{i-1} cell, the probability that it is found in a particular one of the two A_i cells within that A_{i-1} is equal to a constant a that is independent of scale and applies regardless of any prior knowledge of the distribution of that species, such as whether or not it occurs in a neighboring A_{i-1} . It follows that the probability the species is found in just a particular

* Corresponding author; e-mail: aostling@socrates.berkeley.edu.

† E-mail: jharte@socrates.berkeley.edu.

‡ E-mail: jlgreen@ucdavis.edu.

§ E-mail: kinzig@asu.edu.

one of the two A_i cells is $1 - a$, and the probability it is found in both the A_i cells is $2a - 1$. With this rule, the expected species distribution across A_0 can be determined.

Maddux (2004) examined two types of properties of distributions following this PR that he dubbed “biologically unlikely.” The first (discussed in Maddux’s second section, eqq. [6]–[14]) may be summarized as follows: on applying the PR, the fraction of species found throughout certain combinations of cells that result from bisection can equal the fraction found throughout other combinations of cells of a different total area. Even more striking, the fraction of species found throughout certain combinations of cells of a given area can exceed that found throughout combinations of cells of a larger area. Figure 1 illustrates two examples of this, which correspond to Maddux’s equations (7) and (10). The additional examples Maddux examined include cases involving finer scale patches on the left side of the plot (Maddux’s eqq. [12]–[14]), cases involving more of the patches on the plot (Maddux’s eqq. [8], [9]), and cases in which species are found at least in certain locations instead of cases in which species are found only in certain locations (Maddux’s eqq. [6], [9], [11]).

While we arrive at the same result as Maddux for the equalities in figure 1 and throughout his second section, we differ from his conclusion that these relationships (the series of equalities in his eqq. [6]–[14]) all pose a problem. For example, the equality in figure 1A and the first equality in figure 1B are biologically plausible and thus are not logical defects of the PR: they may well be features of actual species distributions that obey a PLSAR. Although these equalities might perceptibly pose a problem because they indicate that the species unique to two regions of differing area are equal, they simply show that under the PR the fraction of species in common to two separated patches decreases with interpatch distance. The decline of similarity in species composition with increasing interpatch distance is prevalent in empirical biogeography studies (Cody 1993; Nekola and White 1999; Condit et al. 2002). In figure 1A, it is plausible that there would be as many species in both the right half and one of the left quadrants as in both left quadrants, since although the former region is larger in area than the latter, it is less geographically clustered. A similar argument can be made for the plausibility of the first of the equalities in figure 1B between the fraction of species indicated by the left-hand diagram and that indicated by the upper right-hand diagram.

The second equality in figure 1B, however, does illustrate a property that seems biologically unlikely. In particular, it says that, under the PR, the fraction of species present in both an octant in the left half and somewhere in the entire right half but nowhere else on the plot is independent of which octant in the left half is chosen. Hence, even

though one octant choice is more clustered geographically with the right half than another, the PR prediction for the expected fraction of species present in both the octant and the right half remains unchanged. So the number of species in common to two patches does not fall off with distance consistently under the PR. This sort of property becomes more clearly unrealistic if examined for even smaller patches, in which case the variation in interpatch distance over the possible placements of the small patch is larger. The general predictions of the PR for the number of species in common to two patches, which can be derived by a procedure analogous to that shown in figure 1B, can be summarized as follows. Let b_j label the bisection lines that divide the cells of size A_{j-1} into cells of size A_j . Any two primary cells of a size A_i that are on the same side of all bisection lines b_1, b_2, \dots, b_{j-1} but on opposite sides of one of the b_j lines will have the same expectation value for the number of species in common. In other words, the order j of the first bisection line that separates the two cells, which we will call the “separation order” of the two cells, determines the number of species they have in common, or their “commonality.” Since pairs of A_i cells can be separated by different distances but have the same separation order, and since pairs of A_i cells can be separated by the same distance but have different separation orders, the PR predicts an inconsistent falloff of commonality with distance, which is biologically unrealistic. Although Maddux included this inconsistency of the falloff of commonality with distance under the PR in equation form in his list of biologically unrealistic properties, he did not emphasize it in the text of his comment. Maddux instead focused on the area independence properties illustrated in figure 1A and the first equality in figure 1B, properties that, as we said above, we do not view as unrealistic.

A second biologically unlikely property of species distributions that follows from the PR is the dependence of species richness in a patch on the location of that patch. This is discussed by Maddux in his third section and is illustrated with a simple example in our figure 2. The PR generates predictions not only for census cells that result from the bisection procedure, which Maddux calls “primary” A_i cells, but also for “secondary” census cells of size A_i that are not the result of the bisection procedure and hence straddle bisection lines that delineate the “primary” A_i . Under the PR, secondary cells of a given area and shape have a different number of species than primary cells of the same area and shape. Figure 2 considers the number of species present in both of the two adjacent A_3 cells that make up a cell of size A_2 but present nowhere else on the plot. As figure 2 shows, the PR predicts that the richness of species of this type is higher in primary A_2 than in secondary A_2 . Maddux considered the total species richness in A_2 and showed that it is lower in primary A_2 than

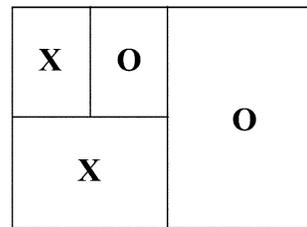
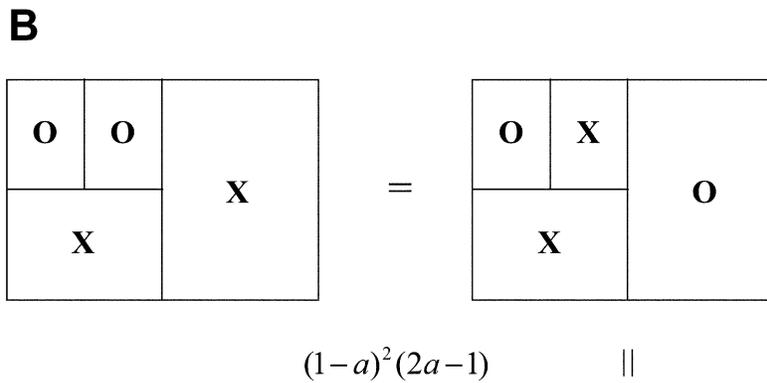
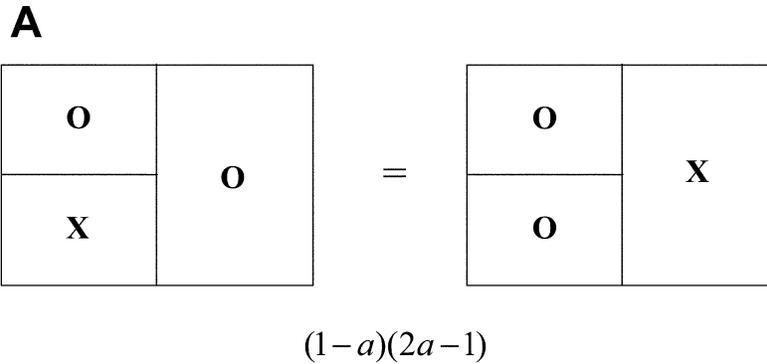


Figure 1: Illustration of the spatial correlation properties predicted by the probability rule (PR), as discussed in Maddux's second section and described in his equations (6)–(14). Only the equality between the upper and lower right-hand diagrams in *B* constitutes a biologically unlikely prediction of the PR. The diagrams indicate the fraction of species found in the cells marked with an *O* but not found in the cells marked with an *X*, and the expressions involving *a* indicate the PR predictions for these fractions. *A*, Corresponds to Maddux's equation (7). For left-hand diagram, the fraction indicated can be obtained by multiplying the probability for a species known to be present somewhere on the landscape to be in both halves, $2a - 1$, by the probability for a species in the left half to be in the lower left quadrant but absent in the upper quadrant, $1 - a$, leading to an expected fraction of species of $(1 - a)(2a - 1)$. For the right-hand diagram, multiply the probability for a species to be present only in the left half, $1 - a$, by the probability for it to be in both quadrants in the left half given that it is in the left half, $2a - 1$, giving $(1 - a)(2a - 1)$. Hence, the expression applies to both diagrams. *B*, Corresponds to Maddux's equation (10). For the left-hand diagram, multiply the probability for a species to be present only in the left half, $1 - a$, by the probability for it to then be only in the upper left quadrant, $1 - a$, and the probability for a species in the upper left quadrant to be in both halves of the upper left quadrant, $2a - 1$, leading to an expected fraction of species of $(1 - a)^2(2a - 1)$. For the upper right-hand diagram, multiply the probability for a species to be in both halves, $2a - 1$, by the probability for it to be in only the upper quadrant in the left half, $1 - a$, and the probability for it to then be in only the left-hand octant in the upper right quadrant, $1 - a$, yielding an expected fraction of species of $(1 - a)^2(2a - 1)$. To calculate the fraction indicated by the lower right-hand diagram, follow the same procedure as the upper right-hand diagram, considering the right-hand octant instead of the left-hand one at the last stage. Hence, the expression applies to all three diagrams.

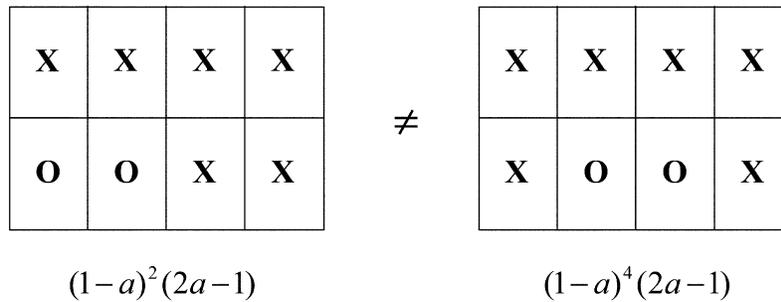


Figure 2: Example of the biologically unlikely locational dependence of species richness predicted by the probability rule (PR), as discussed in Maddux’s third section. The diagrams indicate the fraction of species found in both of the cells marked with an O in the figure but not found in any of the cells marked with an X, and the expressions involving a indicate the PR prediction for these fractions. What is shown is that the PR prediction for the fraction of species present in only two adjacent cells of size $A_3 = A_0/2^3$ within a landscape of size A_0 depends on the location of those cells. In particular, the PR predicts a higher expected fraction of species present in both of the two A_3 cells that form a “primary” A_2 cell, which can be created by repeated bisection of A_0 (left-hand diagram), than in both of the two A_3 cells that form a “secondary” A_2 cell, which cannot be created by repeated bisection of A_0 and hence straddles one of the lines delineating the “primary” A_2 ’s (right-hand diagram). For the left-hand diagram, the fraction of species is given by the probability for a species to be found only in the left half of the figure, $1 - a$, times the probability for it to then be in only the lower part of the left half, $1 - a$, times the probability for it to then be in both halves of the lower left quadrant, $2a - 1$, leading to the expression $(1 - a)^2(2a - 1)$. For the right-hand diagram, the fraction of species is given by the product of the probability for a species to be in both halves of the figure, $2a - 1$, times the probability for the species to then be in only the lower part of the left half, $1 - a$, times the probability for it to be in only the lower part of the right half, $1 - a$, times the probability for it to be in only the right half of the lower left quadrant, $1 - a$, times the probability for it to be in only the left half of the lower right quadrant, $1 - a$, giving $(1 - a)^4(2a - 1)$.

in secondary A_2 . In addition, he provided an extensive analysis of this phenomenon for cells of size A_6 . We agree with Maddux that these types of results pose a genuine problem: the expected species richness of a cell should not depend on its location within the plot. Average species richness should depend at most on size and shape; it should not depend on how one lays out on a landscape the grid that demarcates the cellular structure of the plot. Indeed, we had previously alluded to the problem of such “straddler cells” for species distributions simulated with the PR (Harte 2000).

But an interesting question remains: Is there a way to make predictions about landscape patterns that derive from the PR but that lack the unrealistic features that both we and Maddux agree result from straightforward application of the PR? We suggest that the answer is yes. All theories require “user instructions,” whether implicit or explicit, which inform the user how to use the theory to make contact with observation. When applying the PR to predict species richness, an instruction that enables the user to avoid unrealistic predictions is as follows: Predict the expected species richness in any cell or set of cells of size and shape A_i (even secondary cells that do not result from bisection) by using the PR to generate the expectation value for the species richness in A_i that results from bisection (i.e., “primary” A_i). When applying the PR to look at the falloff of commonality with distance, instructions that will enable the user to avoid obviously unrealistic predictions are as follows: Apply the PR to a landscape of

shape $L \times L(2^{1/2})$ to predict $N(A_i, D_j)$, the expected number of species in common to two cells of size and shape A_i separated by the distances $D_j = L/(2^{j/2})$. Predict $N(A_i, D_j)$ by generating the PR expectation value for the number of species in common to a pair of A_i that has “separation order” j (i.e., A_i that are on the same side of all bisection lines b_1, b_2, \dots, b_{j-1} but on opposite sides of one of the b_j lines). Such a pair of A_i ’s will on average have their centers separated by approximately D_j , the distance for which the commonality prediction is being made, with a correction factor that depends slightly on the scale i . By associating prediction distance for a pair of cells with the pair’s separation order, which determines its commonality, this user rule yields a consistent falloff of commonality with distance. Augmented with these instructions, the PR provides a realization of a fractal landscape that makes contact with observation and does not generate the obviously unrealistic patterns pointed out by Maddux.

The Equivalence of the Power Law Species-Area Relationship and a Community Fractal Property

Another issue raised by Maddux’s work is whether the unrealistic properties that stem from the PR undermine the relationship between a fractal property and the PLSAR claimed in Harte et al. (1997, 1999b). To resolve this issue, we next show that the PLSAR is equivalent to a community fractal property (CFP) that is more general than the probability rule (PR) discussed by Maddux. Because of the

equivalence of this CFP with the PLSAR, it implies no unrealistic patterns. We begin by showing the equivalence of these properties for patches created by bisection and then show that this equivalence holds more generally for a continuous set of patch sizes. We will be using the term “species occurrence,” by which we mean simply an instance of a species being present in an A_i cell.

Consider a cell randomly selected from the set of A_{i-1} cells and a species occurrence (at $i-1$ scale) randomly chosen from the set of species occurrences in that cell. We define a_i to be the probability that this species occurrence is also present in a particular (say the left-hand) one of the two cells of area A_i contained in the selected A_{i-1} cell. The distribution of species is fractal at the community level if a_i is independent of i , that is, if $a_i = a$ for all i .

Note that under this community fractal property (CFP), the probability a is applicable to a species occurrence at the $i-1$ scale that is drawn at random from all such species occurrences within A_0 . This probability may or may not accurately describe subsets of all of the species occurrences in cells of size A_{i-1} that are not randomly selected, such as the occurrences of just one particular species, or species occurrences in A_{i-1} cells adjacent to cells in which the chosen species also occurs. The PR, which uses the probability a to distribute every species in every A_{i-1} regardless of any other knowledge of the distribution of that species, does not follow from the CFP. However, if species are distributed according to the PR, the CFP will hold on the “primary” patches (those created by the bisection procedure). Note also that the CFP is different from an assumption that each species has a constant density across A_0 . The CFP can describe a range of clustering patterns in species distributions through the range of values for the probability a . Recall that $2a-1$ is the probability a species is found in both halves of a cell in which it is present. At the extremes are the case $a = 0.5$ (giving $2a-1 = 0$), in which each species is present in only one A_i in A_0 and hence species have tightly clustered distributions, and the case $a = 1$ (giving $2a-1 = 1$), in which each species is in every A_i throughout A_0 and hence species are uniformly distributed.

To show the equivalence of this CFP with the PLSAR, we first derive an expression for a_i based on that the fact that the probability of an event can be estimated as the number of trials for which the event happens divided by the total number of trials. How many trials are possible? Recalling that in the entire region A_0 there are $2^{i-1}A_{i-1}$ cells, that they contain on average S_{i-1} species, and that there are two trials for every species occurrence (one for each of the two A_i within an A_{i-1}), there are $2 \times 2^{i-1} \times S_{i-1}$ trials. The event whose probability we seek happens for every species occurrence in an A_i cell, and hence there are $2^i \times S_i$ such events. Hence,

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

If we assume that the CFP holds, that is, that a_i is independent of i , then, using this expression for a_i in equation (1), it follows that the average species richness, averaged over all cells of area A_i , is given by $S_i = a^i S_0$, where the symbol a^i refers to a raised to the power i . Writing $a_i = 2^{\log_2(a)}$ and using the fact that $A_i/A_0 = 2^{-i}$, this expression for the average species richness at scale i becomes

$$S_i = S_0 \left(\frac{A_i}{A_0} \right)^{-\log_2(a)}. \quad (2)$$

Defining $z = -\log_2(a)$, the more standard form of the power law species-area relationship (SAR),

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

follows with $c = S_0/A_0^z$. Hence, the CFP implies that the average species richness on the A_i cells satisfies the power law form of the SAR.

The logic is reversible. Given that $S_i = cA_i^z$, it follows from equation (1) that $a_i = (A_i/A_{i-1})^z = 2^{-z}$, which is independent of i . Thus, so long as the power law SAR holds for the average species richness across the discrete set of A_i cells formed by bisections, then there must be a community-level probability parameter a that applies to the average distribution of species in these cells and is independent of the scale parameter i . Because z can, in principle, take on a continuum of values between 0 and 1, a can take on a continuum of values between 0.5 and 1.

So far we have shown the equivalence of the PLSAR and the CFP on the discrete set of patches A_i formed from a patch of size A_0 by i bisections. Does this equivalence hold more generally for patch sizes in between A_{i-1} and A_i ? In his appendix A, Maddux discusses the fact that the PR implies PLSAR only on the discrete set of patch sizes A_i ; that is, it only implies the discrete power law $S_i = cA_i^z$. We agree with Maddux’s presentation of the relationship between the PR and PLSAR. However, the equivalence of the more general CFP with the PLSAR is not limited to discrete patches: the answer to the question we posed is yes. We will now show that the PLSAR on patches of size $A_i = A_0/b^i$, where b can be noninteger, is equivalent to a CFP on those same patches with a probability parameter $a = b^{-z}$. Since any positive real number b can be chosen, this means that the PLSAR is equivalent to a CFP for a continuous set of patch sizes.

We define n_l to be the integer number of patches of size A_i that are entirely inside the l th patch of size A_{i-1} (these

patches will not necessarily completely cover an A_{i-1} patch). This number n_i will depend on the particular way the A_i patches are located within that A_{i-1} patch. The method of location need not be consistent from one A_{i-1} patch to another, nor from one scale transition to another, and the patches A_i can overlap. We can define a CFP on this set of patches as follows. Consider a randomly chosen patch of size A_{i-1} (labeled l) and a species randomly chosen from those that occur in that A_{i-1} (i.e., consider a randomly chosen “species occurrence” at the $i - 1$ scale). We define a_i to be the probability that the chosen species also occurs in a particular one of the n_i patches of size A_i within that A_{i-1} . The distribution of species is fractal at the community level (i.e., it exhibits the CFP) if this probability is scale invariant, that is, if $a_i = a$ for all i .

Similar to the bisection case, we can use the fact that the probability of an event can be estimated as the number of trials for which the event happens, divided by the total number of trials, to write an expression for a_i in terms of the mean species richness at scales $i - 1$ and i . In the following, we will use $S_{i-1,l}$ to denote the number of species in the l th patch of size A_{i-1} , that is, in the patch $A_{i-1,p}$ and S_{i-1} to denote the average number of species across all patches of size A_{i-1} , that is, $S_{i-1} = \langle S_{i-1,l} \rangle_l$ where $\langle \rangle_l$ indicates an average the different patches labeled by l . There are n_i trials at scale i for every species occurrence in $A_{i-1,p}$ the l th sampling patch at the $i - 1$ scale. Hence, the total number of trials at scale i is $\sum_l (n_i \cdot S_{i-1,l})$. The event happens for every species occurrence in an A_i . The total number of species occurrences in cells of size A_i is S_p , the average species richness over all cells of size A_p , times $\sum_l n_p$, the total number of cells of size A_p . The probability a_i is just the ratio of this number of events to the total number of trials:

$$a_i = \frac{(\sum_l n_i) \cdot S_i}{\sum_l (n_i \cdot S_{i-1,l})} = \frac{(\sum_l n_i) \cdot S_i}{(\sum_l n_i) \cdot S_{i-1}} = \frac{S_i}{S_{i-1}}. \quad (4)$$

The second equality in equation (4) arises by assuming that n_i and $S_{i-1,l}$ are uncorrelated, in which case the average of the product of n_i and $S_{i-1,l}$ is equal to the product of the separate averages of n_i and of $S_{i-1,l}$ (we denote this latter average simply by S_{i-1}). This will be a valid assumption as long as the number of sampling patches used in a particular spot on the landscape is not determined by the species richness in that location. Clearly, if the same number of A_i patches are considered within each A_{i-1} patch (i.e., if n_i is independent of l), this assumption is satisfied.

The equivalence between the PLSAR and the CFP across the patches just described of size $A_i = A_0/b^i$, where b is any positive real number, can be shown in a way analogous

to the bisection case. If we assume that the CFP holds, that is, that a_i is independent of i , then, using equation (4), it follows that the average species richness, averaged over all cells of area A_p , is given by $S_i = a^i S_0$, where the symbol a^i refers to a raised to the power i . Writing $a_i = b^{\log_b(a)}$ and using the fact that $A_i/A_0 = b^{-i}$, this expression for the average species richness at scale i becomes

$$S_i = S_0 \left(\frac{A_i}{A_0} \right)^{-\log_b(a)}. \quad (5)$$

Defining $z = -\log_b(a)$, the PLSAR $S_i = cA_i^z$ follows with $c = S_0/A_0^z$. Conversely, if we assume the PLSAR, it follows from equation (4) that $a_i = (A_i/A_{i-1})^z = b^{-z}$, which is independent of i , and hence the CFP holds. Since any positive real number can be chosen for b , the PLSAR and CFP are equivalent for a continuous set of patch sizes. In particular, they are equivalent even for patch sizes between those that can be obtained by bisection of the plot, as long as the fractal parameter a is appropriately defined in terms of the parameter b that describes the patch size.

Empirical studies suggest that the relationship between species richness and area has shape dependence (Kunin 1997; Harte et al. 1999a). In order to avoid the confounding effects of shape, one must examine the relationship between species richness and area for patches that are all of the same shape. In his appendix D, Maddux illustrates the problems that arise when shape and area vary simultaneously in an application of the PR. In defining the CFP that is equivalent to the PLSAR, one must also define it for patches that are all of the same shape. Harte et al. (1997, 1999a) considered patches of shape $2^{1/2} \times 1$ because this allowed use of a simple bisection algorithm for creating patches of different size but the same shape. In our proof of the more general equivalence of the PLSAR and the CFP for a continuous set of patch sizes, it is not necessary to constrain the shape that can be chosen for patches, but we do mean for shape to be held constant across the patches in order to avoid these confounding effects of shape on species richness.

Concluding Remarks

Clarifying the relationship between the power law species-area relationship (PLSAR) and fractals is important because self-similarity has been used not only to provide insight into the PLSAR but also to connect the species-area relationship to other measurable types of patterns in the distribution and abundance of species (Harte and Kinzig 1997; Harte et al. 1999a, 1999b, 2001; Ostling et al. 2000; Green et al. 2003; Sizing and Storch 2004). Maddux (2004) points out that a self-similarity probability rule

q4

q5

(PR), which has been used to create landscapes that exhibit the PLSAR, makes biologically unrealistic predictions. Hence, Maddux calls into question the relationship between the PLSAR and fractals. Although we agree with Maddux that the PR makes biologically unrealistic predictions, we have shown here that there is a community-level fractal property (CFP) that is mathematically equivalent to the PLSAR and that this CFP is more general than the PR: the PR is just one way to realize a landscape for which the CFP holds. Thus, a tight relationship exists between the PLSAR and a fractal property, despite the failures of the PR.

Yet in order for ecologists to connect the PLSAR with other measurable characteristics of the distribution of species, they may need a method for creating landscapes that exhibit the CFP. We have argued here that despite the failings of the PR, it may still provide a realistic model of species distributions that exhibit the PLSAR, if supplemented with instructions that enable the user to avoid predictions that are obviously biologically unlikely. But the predictions of the PR for the spatial scaling of endemism and species abundance, predictions that are not obviously biologically unlikely, have been shown to fail empirically at least in one system (Green et al. 2003). Hence, an important future research direction will be to uncover methods alternative to the PR for realizing landscapes that exhibit the CFP.

Acknowledgments

Support to J.L.G. in the form of a National Science Foundation postdoctoral fellowship and to J.H. and A.O. from the University of California Berkeley Class of 1935 Distinguished Professorship are gratefully acknowledged.

Literature Cited

- Cody, M. L. 1993. Bird diversity components within and between habitats in Australia. Pages 147–158 in R. Ricklefs and D. Schluter, eds. *Species diversity in ecological communities*. University of Chicago Press, Chicago.
- Condit, R., N. Pitman, E. G. Leigh, J. Chave, J. Terborgh, R. B. Foster, P. Nunez, et al. 2002. Beta-diversity in tropical forests. *Science* 295:666–669.
- Gaston, K., and T. Blackburn. 2000. *Pattern and process in macroecology*. Blackwell Scientific, Oxford.
- Green, J. L., J. Harte, and A. Ostling. 2003. Species richness, endemism, and species abundance: tests of two fractal models in a serpentine grassland. *Ecology Letters* 6:919–928.
- Harte, J. 2000. Scaling and self similarity in species distributions: implications for extinction, species richness, abundance, and range. Pages 325–342 in J. H. Brown and G. B. West, eds. *Scaling in biology*. Oxford University Press, Oxford.
- Harte, J., and A. P. Kinzig. 1997. On the implications of species-area relationships for endemism, spatial turnover, and food web patterns. *Oikos* 80:417–427.
- Harte, J., S. McCarthy, K. Taylor, A. Kinzig, and M. Fischer. 1999a. Estimating species-area relationships from plot to landscape scale using species spatial-turnover data. *Oikos* 86:45–54.
- Harte, J., A. Kinzig, and J. Green. 1999b. Self-similarity in the distribution and abundance of species. *Science* 284:334–336.
- Harte, J., T. Blackburn, and A. Ostling. 2001. Self-similarity and the relationship between abundance and range size. *American Naturalist* 157:374–386.
- Kunin, W. 1997. Sample shape, spatial scale, and species counts: implications for reserve design. *Biological Conservation* 82:369–377.
- Maddux, R. 2004. Self-similarity and the species-area relationship. *American Naturalist* 163:XXX–XXX.
- Nekola, J. C., and P. S. White. 1999. The distance decay of similarity in biogeography and ecology. *Journal of Biogeography* 26:867–878.
- Ostling, A., J. Harte, J. Green, and A. Kinzig. 2003. A community-level fractal property produces power law species-area relationships. *Oikos* 103:218–224.
- Sizling, A. L., and D. Storch. 2004. Power-law species-area relationships and self-similar species distributions within finite areas. *Ecology Letters* 7:60–68.

Associate Editor: Jonathan B. Losos

QUERIES TO THE AUTHOR

1 I have changed boldface \mathbf{a} to a throughout text (per Press style, bold italic generally indicates vectors). Is change OK?

2 Harte et al. 1997 is not listed in "Literature Cited." Should this be changed to Harte and Kinzig 1997? If not, please provide reference information or delete from text. (Citation also appears in paragraph before "Concluding Remarks.")

3 I revised the sentence that begins "This probability" to avoid awkward phrasing ("non-randomly selected"). Is change OK?

4 Should the sentence that begins "In the following" be revised to read "an average of the different patches"?

5 Ostling et al. 2000 is not listed in "Literature Cited." Should this be changed to 2003? If not, please provide reference information or delete from text.

6 Gaston and Blackburn 2000 is not cited in the text. Please provide in-text citation or delete from "Literature Cited."

The American Naturalist

Kelli Morrison
The University of Chicago Press
1427 East 60th Street
Chicago, IL 60637

Offprint Order Form

Please return this form even
if no offprints are ordered.

NO OFFPRINTS ORDERED

AUTHORS: OFFPRINT ORDER MUST BE RECEIVED PRIOR TO PRINTING OF JOURNAL ISSUE. Please return this form immediately even if no offprints are desired. Offprints ordered through an institution will not be processed without a purchase order number. Payment by check, Money Order, Visa, or MasterCard is required with all orders not accompanied by an institutional purchase order or purchase order number. **Make checks and purchase orders payable to The University of Chicago Press.**

TO BE COMPLETED BY AUTHOR:

The American Naturalist Vol _____ No _____ Month _____ Year _____

Author(s): _____ No of pages in article _____

Title of Article: _____

OFFPRINT PRICE LIST: Prices include UPS domestic shipping. Non-U.S. orders are shipped via Airmail at an additional cost of 45% of the total printing charge.

Pages	Total Quantity					add'l Charges (please compute)	
	50	100	150	200	50's		
2-4	\$64.00	\$76.00	\$89.00	\$100.00	\$11.00	_____ Quantity	\$ _____
5-8	71.00	91.00	110.00	129.00	19.00	Covers	\$ _____
9-12	77.00	111.00	139.00	167.00	28.00	Subtotal	\$ _____
13-16	86.00	123.00	156.00	190.00	34.00	GST (7% for Canadian destinations only)	\$ _____
17-20	98.00	146.00	190.00	234.00	44.00	Non-U.S. Shipping	
21-24	105.00	161.00	214.00	267.00	53.00	(Non-U.S. orders add 45% to subtotal)	\$ _____
addl 4 pgs	21.00	39.00	55.00	71.00	16.00		
Covers	93.00	105.00	123.00	140.00	19.00	TOTAL DUE (US \$)	\$ _____

Shipping Instructions

Name _____
Phone* _____ Fax _____
Dept _____ Room _____
Institution _____
Street _____
City _____ State _____ Zip _____
Country _____

Billing Instructions (Institutional Orders Only; must have PO)

Institution _____
Street _____
City _____ State _____ Zip _____
Country _____
Phone _____
email _____

* Please include a phone number in case we need to contact you about your order.

MAKE CHECKS AND PURCHASE ORDERS PAYABLE TO: The University of Chicago Press

All orders must be accompanied by one of the three payment options (purchase order, check/money order, or Visa/MasterCard):

1) Institutional Purchase Order No. _____ Purchase Order attached to come

Order will not be processed without a number.

2) Check or money order for total charges is attached **OR** 3) Please charge to: VISA MASTERCARD

Cardmember name as it appears on card (please print clearly) _____

Card Number _____ Expiration Date _____

Signature _____ Phone _____

RETURN THIS OFFPRINT ORDER FORM **WITH YOUR PROOFS** TO:

THE AMERICAN NATURALIST
Kelli Morrison
The University of Chicago Press
1427 East 60th Street
Chicago, IL 60637
Phone: 773-702-7487

OFFPRINT INSTRUCTIONS:

DO NOT DELAY ORDERING YOUR OFFPRINTS. Orders must be in hand before the issue goes to press.

DELIVERY AND INVOICES Offprints are shipped 2-4 weeks after publication of the journal. Invoices are mailed at the time of shipment. **For all orders charged to institutions, an official Purchase Order must be in hand before the offprint shipment can be released.** Offprint orders payable by individuals must be accompanied by advance payment by check, money order, Visa, or MasterCard. In case of non-U.S. purchases, this payment must be made in the form of a check payable in U.S. currency via an American bank.

Terms are net 30 days.