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

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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. (1999) 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 $A_i$ is a $2^{i/2} \times 1$ 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
one of the two $A_i$ cells is $1 - a$, and the probability it is found in both the $A_j$ cells is $2a - 1$. With this rule, the expected species distribution across $A_i$ 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 perceivably 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 hand 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 $A_{i,j}$ 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 $b_j$, $b_3$, …, $b_{l-1}$, 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 $A_j$ 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 $A_j$ 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 $A_i$ cells that make up a cell of size $A_j$ 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 $A_j$ than in secondary $A_j$. Maddux considered the total species richness in $A_j$ and showed that it is lower in primary $A_j$ 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 $(1-a)^3(2a-1)$. 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.
in secondary $A_r$. In addition, he provided an extensive analysis of this phenomenon for cells of size $A_r$. 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 $N(A_i, D)$, the expected number of species in common to two cells of size and shape $A_i$ separated by the distances $D_i = L(2^{1/2})$. Predict $N(A_i, D_i)$ 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 $b_1, b_2, \ldots, b_{j-1}$ 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

**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 X in the figure but not found in any of the cells marked with an O, 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 $A_i = A_i/2^1$ within a landscape of size $A_i$ depends on the location of those cells. In particular, the PR predicts a higher expected fraction of species present in both of the two $A_i$ cells that form a “primary” $A_i$ cell, which can be created by repeated bisection of $A_i$, (left-hand diagram), than in both of the two $A_i$ cells that form a “secondary” $A_i$ cell, which cannot be created by repeated bisection of $A_i$ and hence straddles one of the lines delineating the “primary” $A_i$’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, $(1 - a)(2a - 1)$, 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 left quadrant, $1 - a$, times the probability for it to be in only the lower part of the right half, $(1 - a)^2(2a - 1)$, leading to the expression $(1 - a)^4(2a - 1)$.
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 a $A_i$ 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 $A_i$. 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 $\theta$ 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 $A_i$. 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 $A_o$ 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 $A_o$ 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 $A_o$ 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 $S_i = a_i S_o$, where the symbol $a'$ refers to $a$ raised to the power $i$. Writing $a_i = 2^{\log_2(a)}$ and using the fact that $A_i/A_o = 2^{-i}$, this expression for the average species richness at scale $i$ becomes

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

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 $c = S_o/A_o^z$. 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 $A_o$ 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 $A_i = A_o/b^i$, 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 $n_i$ to be the integer number of patches of size $A_i$ that are entirely inside the $i$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 \( A_{i-1,b} \). 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 \( S_{i-1} \), to denote the number of species in the \( h \)th patch of size \( A_{i-1} \), that is, in the patch \( A_{i-1,b} \) and \( S_{i-1} \) to denote the average number of species across all patches of size \( A_{i-1} \), that is, \( S_{i-1} = \langle S_{i-1,b} \rangle \) where \( \langle \rangle \) indicates an average the different patches labeled by \( l \). There are \( n_i \) trials at scale \( i \) for every species occurrence in \( A_{i-1,b} \), the \( h \)th sampling patch at the scale \( i-1 \). The event happens for every species occurrence in an \( A_i \). The total number of species occurrences in cells of size \( A_i \) is \( S_b \), the average species richness over all cells of size \( A_i \), times \( \sum_i n_i \), the total number of cells of size \( A_i \). The probability \( a_i \) is just the ratio of this number of events to the total number of trials:

\[
    a_i = \frac{\langle \sum_i n_i \cdot S_{i-1,b} \rangle \cdot S_b}{\sum_i n_i \cdot S_{i-1}} = \frac{\langle \sum_i n_i \cdot S_{i-1,b} \rangle \cdot S_{i-1}}{\langle \sum_i n_i \cdot S_{i-1} \rangle} = \frac{S_{i-1}}{S_{i-1}}.
\]

The second equality in equation (4) arises by assuming that \( n_i \) and \( S_{i-1} \) are uncorrelated, in which case the average of the product of \( n_i \) and \( S_{i-1} \) is equal to the product of the separate averages of \( n_i \) and of \( S_{i-1} \) (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 \( A_i = A_{i-1}/b^i \), 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 \( A_i \) is given by \( S_i = a'S_{b0} \) where the symbol \( a' \) refers to \( a \) raised to the power \( i \). Writing \( a_i = b^{-\log_i(a)} \) and using the fact that \( A_i/A_{b0} = b^{-i} \), this expression for the average species richness at scale \( i \) becomes

\[
    S_i = S_{b0} \left( \frac{A_i}{A_{b0}} \right)^{-\log_i(a)}.
\]

Defining \( z = -\log_i(a) \), the PLSAR \( S_i = cA_i^z \) follows with \( c = S_{b0}/A_{b0}^z \). Conversely, if we assume the PLSAR, it follows from equation (4) that \( a_i = (A_i/A_{b0})^z = b^{-i} \), 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; Sizling and Storch 2004). Maddux (2004) points out that a self-similarity probability rule...
(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.

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Literature Cited


QUERIES TO THE AUTHOR

1 I have changed boldface \textit{a} to \textit{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.”
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| 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) $(________) |
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| addl 4 pgs | 21.00 | 39.00 | 55.00 | 71.00 | 16.00 | TOTAL DUE (US $) $(________) |
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