Notes

ENDEMICS–AREA RELATIONSHIPS: THE INFLUENCE OF SPECIES DOMINANCE AND SPATIAL AGGREGATION

Jessica L. Green[1,3] and Annette Ostling[2]

[1]*Department of Biological Sciences, Macquarie University, NSW 2109 Australia*
[2]*Energy and Resources Group, University of California, Berkeley, California 94720 USA*

Abstract. Patterns in the spatial distribution of endemic species are central to setting conservation priorities and estimating extinction rates due to habitat loss. We use quantitative models to isolate the effects of relative species abundances and conspecific spatial distributions on the endemics–area relationship. Using published abundance data from a tropical rain forest community, we apply these models to illustrate how species abundance distributions and species spatial distributions have a strikingly different influence on total and endemic species diversity patterns, respectively. Increased dominance and conspecific aggregation in a region will act to decrease the total species diversity of smaller sampled subregions, but to increase subregional endemic species diversity. Our results suggest that biotic or abiotic forces contributing to regional-scale species dominance and conspecific clustering may increase the risk of extinctions under habitat loss.

Key words: abundance; aggregation; dominance; endemics; endemics–area relationship; evenness; extinction risk; negative binomial; random placement; spatial distribution; species–area relationship.

INTRODUCTION

Patterns in the spatial distribution of endemic species, species with geographic distributions limited to a specified region, are central to our understanding and conservation of biological diversity. Regions featuring high concentrations of narrowly distributed species (centers of endemism) are frequently targeted as priority conservation areas because species with small geographical ranges are potentially at a greater risk of extinction than those with larger ranges (Bibby et al. 1992, Mittermeier et al. 1998, Myers et al. 2000). However, recognition of centers of endemism is dependent on the scale of the study region (Major 1988, Anderson 1994). For example, although the continent of Australia is recognized as a major center of endemism, large regions within the continent such as southwest Western Australia are also recognized as centers of endemism (Crisp et al. 2001). Hence, the need to identify and compare patterns of endemism across different spatial scales when setting national or global conservation priorities is becoming increasingly recognized (Peterson and Watson 1998). An understanding of the relationship between the number of species endemic to a region and the area of that region, the endemics–area relationship (EAR), is pivotal to such comparisons.

In addition to targeting conservation areas, understanding patterns in the spatial distribution of endemic species is critical to estimating extinction rates due to habitat loss. Although species–area relationships have traditionally been applied to estimate extinction rates following habitat loss, it is now understood that applying EARs can yield very different and perhaps more accurate predictions (Kinzig and Harte 2000, Green et al. 2001, Zurlini 2002).

Despite the important role of endemism in conservation biology, there have been few theoretical or modeling advances examining the relationship between endemic species richness and area. Existing theory regarding EARs assumes that the spatial distribution of species is fractal, or self-similar (Harte and Kinzig 1997, Harte et al. 1999). The form of the EAR under a more general array of species spatial and abundance distributions has yet to be examined. In particular, under the fractal approach, a species abundance and the spatial aggregation of its individuals are both a function of the fractal dimension of the species distribution, and hence one cannot assess independently the influence of species relative abundances and intraspecific clustering on the EAR.

[3] Present address: Department of Environmental Science and Policy, University of California, One Shields Avenue, Davis California 95616 USA. E-mail: jlgreen@ucdavis.edu

TABLE 1. Species-abundance models and the corresponding endemics–area curves under the assumption that all species in a community are randomly distributed.

Species-abundance model	Specification	Endemics–area curve
Most even	$n_1 = n_2 = \cdots = n_S = \dfrac{N}{S}$	$E(a) = S\left(\dfrac{a}{A}\right)^{N/S}$
Broken-stick	$s_n = \dfrac{S(S-1)(1-n/N)^{S-2}}{N}$	$E(a) = \displaystyle\sum_{n=1}^{\infty}\left(\dfrac{a}{A}\right)^n s_n$
Geometric	$n_i = \dfrac{NK(1-K)^{i-1}}{1-(1-K)^S}$	$E(a) = \displaystyle\sum_{i=1}^{S}\left(\dfrac{a}{A}\right)^{n_i}$
TNBD	$s_n = \dfrac{\Gamma(\gamma+n)}{n!\Gamma(n)}\left(\dfrac{\phi}{1+\phi}\right)^n\dfrac{1}{(1+\phi)^\gamma - 1}$	$E(a) = S - \dfrac{S}{1-(1+\phi)^{-\gamma}}\left\{1 - \left[1 + \phi\left(1 - \dfrac{a}{A}\right)\right]^{-\gamma}\right\}$
Log series	$s_n = \alpha\dfrac{x^n}{n}$	$E(a) = -\alpha\ln\left(1 - \dfrac{ax}{A}\right)$
Most uneven	$n_1 = n_2 = \cdots = n_{S-1} = 1, \qquad n_S = N - S + 1$	$E(a) = (S-1)\dfrac{a}{A} + \left(\dfrac{a}{A}\right)^{N-S+1}$

Notes: All parameters follow the notation of He and Legendre (2002: Table 1). N is the total number of individuals in the entire community with area A; S is the total number of species. In the specification column, s_n is the number of species (broken-stick, log series) or probability function (TNBD) with n individuals for a corresponding species–abundance model. In the right-hand column, $E(a)$ is the expected number of endemic species in the sampling area a. For the geometric series, n_i is the number of individuals of the ith species for $i = 1, 2, \ldots, S$; K is the resource preemption parameter. For the truncated negative binomial distribution (TNBD), γ is the shape parameter measuring the shape of the species–abundance distribution, and ϕ is the scale parameter. For the log-series distribution, α and x are parameters.

In this paper, we use quantitative models to clarify the influences of sampling area, species abundances, and intraspecific clustering on endemic species diversity. Our analysis is motivated by a recent study of He and Legendre (2002), who explored the influences of sampling area, species abundances, and interspecific clustering on total species diversity. Paralleling He and Legendre's study, we use a random placement model to isolate the effects of relative species abundance on the EAR, and a nonrandom placement model to study the effects of spatial distribution on the EAR. Using parameters estimated from a tropical rain forest community, we compare species–area and endemics–area curves under a variety of different species abundance and spatial distribution scenarios.

ENDEMICS–AREA MODELS UNDER RANDOM DISTRIBUTION

Here we assume, as He and Legendre (2002) did, that all of the individuals of a set of S species with abundances $\{N_i, i = 1, 2, \ldots, S\}$ are independently and randomly distributed throughout a region or biome of area A. The probability of finding a particular individual of a species in a smaller region of area a within A is a/A. The probability of finding all N_i individuals of a species in subregion a is $(a/A)^{N_i}$. The expected number of species endemic to subregion a, $E(a)$, is the sum across all species of this probability:

$$E(a) = \sum_{i=1}^{S}\left(\frac{a}{A}\right)^{N_i}. \qquad (1)$$

If the set of S species are globally endemic to A (found in A and nowhere else), then $E(a)$ represents the expected number of species globally endemic to subregion a. If the set of S species includes species that may be present outside of A, then $E(a)$ represents the expected number of species locally endemic to a, meaning species confined to subregion a within A, and hence found nowhere else in A. In this paper, we aim to illustrate that the effects of relative abundance and spatial aggregation on the species–area relationship found by He and Legendre (2002) are entirely the opposite of the effects of these factors on the endemics–area relationship. Hence, we use the same abundance distribution parameters as He and Legendre (2002: Table 1), those fitted to data for all species in a 500×1000 m plot of the Pasoh Forest Reserve, Malaysia, and we plot the *local* endemics–area relationships that would result at this site under different scenarios. However, our analyses and conclusions are equally relevant to scaling patterns of *global* endemism.

Effect of species dominance on endemic species richness

Using Eq. 1, one can examine how different relative abundances across the S species in A, with varying

degrees of dominance (or evenness, which is the complement of dominance), will give rise to different numbers of endemic species in subregion a. Given a fixed number of species (S) and total individuals (N) within A, a community characterized by the most even species-abundance distribution will have N/S individuals per species. A decrease in evenness will result in an increase in rarity (or an increase in the number of species with abundance less than N/S). In the case of random placement, the likelihood that a species would be confined to a subregion a increases with decreased abundance of the species; thus, one would expect a decrease in evenness to be coupled with an increase in endemic species diversity.

To numerically evaluate the effect of dominance on the endemics–area curve, we used two different sets of species-abundance models. First, we plotted the random-placement endemics–area curves for each species-abundance model in Table 1 (Fig. 1); these curves vary in their level of evenness at the regional scale. For each species-abundance model, we used the estimated parameters fit to data from the Pasoh Forest Reserve, Malaysia (He and Legendre 2002: Table 2). For this data set, there are, in total, 814 species and 335 356 individuals within a 500 × 1000 m rectangular plot ($S = 814$, $N = 335\,356$, and $A = 500\,000$ m²). The actual observed abundance distribution for this data set falls between the broken-stick and geometric-series abundance distributions with respect to evenness.

Overall, Fig. 1 illustrates that a decrease in evenness at the regional scale leads to an increase in endemic species diversity in a subregion a, but a decrease in total species diversity in that subregion. However, there are different measures of evenness. With the Pielou metric J' (Pielou 1975), evenness decreases monotonically from the most even distribution through the broken-stick, TNBD (truncated negative binomial), geometric, and log series distributions to the most uneven distribution (He and Legendre 2002: Table 2), and endemic species richness increases systematically through this series. By contrast, evenness does not decrease monotonically through this series of distributions if measured by Gini's coefficient g (Weiner and Solbrig 1984); hence, endemic species richness does not increase systematically with evenness as measured by Gini's coefficient.

In Fig. 2, we plotted the random-placement endemics–area curves for a set of landscape-scale species-abundance distributions that, as He and Legendre pointed out, is monotonic in both of these measures of evenness. This second species-abundance model divides the total abundance across all species (N) in such a way that each of the first S_0 species has only one individual, whereas the remaining $N - S_0$ individuals are split equally among the remaining $S - S_0$ species. For this example, we used $S_0 = 0$ (most even), $S_0 = 250$, $S_0 = 550$, and $S_0 = 813$ (most uneven). And, as before, we assumed that $S = 814$, $N = 335\,356$, and $A = 500\,000$ m². Fig. 2 further validates the expected pattern that increased species dominance in the large region A (a decrease in evenness) results in increased endemic species richness within a subregion a.

ENDEMICS–AREA MODELS UNDER NONRANDOM DISTRIBUTION

Here we assume, as did He and Legendre (2002), that the individuals of the set of S species with abundances $\{N_i, i = 1, 2, \ldots, S\}$ are distributed such that the probability of species i being present in a subregion of area x is independent of the spatial distribution of all other species and equal to:

$$p_i(x) = 1 - \left(1 - \frac{x}{A}\right)\left(1 + \frac{N_i x}{Ak_i}\right)^{-k_i}. \quad (2)$$

Here, the parameter k_i characterizes the spatial distribution of species i and can take on values in the intervals $(-\infty, -N_i x/A)$ and $(0, \infty)$. Note that $N_i x/A$ is the average abundance of the species in area x. When k_i is negative, $p_i(x)$ describes a regular spatial distribution of individuals; when k_i is positive, $p_i(x)$ describes an aggregated spatial distribution of individuals. The degrees of regularity and aggregation each decrease with increasing magnitude of k_i. Under this model of intraspecific aggregation, the expected number of species in a subregion of size a is the sum over species of $p_i(a)$:

$$S(a) = \sum_{i=1}^{S} p_i(a) = S - \left(1 - \frac{a}{A}\right)\sum_{i=1}^{S}\left(1 + \frac{N_i a}{Ak_i}\right)^{-k_i}. \quad (3)$$

The probability that a species would be endemic to an area of size a is the same as the probability that it would be absent from an area $A - a$. This probability is simply $1 - p_i(A - a)$. Hence, the number of endemic species in an area of size a is

$$E(a) = \sum_{i=1}^{S} [1 - p_i(A - a)]$$

$$= \left(\frac{a}{A}\right)\sum_{i=1}^{S}\left[1 + \frac{N_i(A - a)}{Ak_i}\right]^{-k_i}. \quad (4)$$

The two ends of the endemics–area relationship are fixed: $E(0) = 0$ and $E(A) = S$. When all $k_i = -N_i x/A = (-N_i(A - a)/A)$, the species are so regularly distributed in the subregion of size $A - a$ that every species is almost certainly present in $A - a$, resulting in $E(A - a) = S$ and $E(a) = 0$.

With the factor $1 - x/A$ replaced by 1, Eq. 2 is a model of spatial distribution derived from a binomial distribution for $k_i < -N_i x/A$ and from the negative binomial distribution for $k_i > 0$. Although the negative
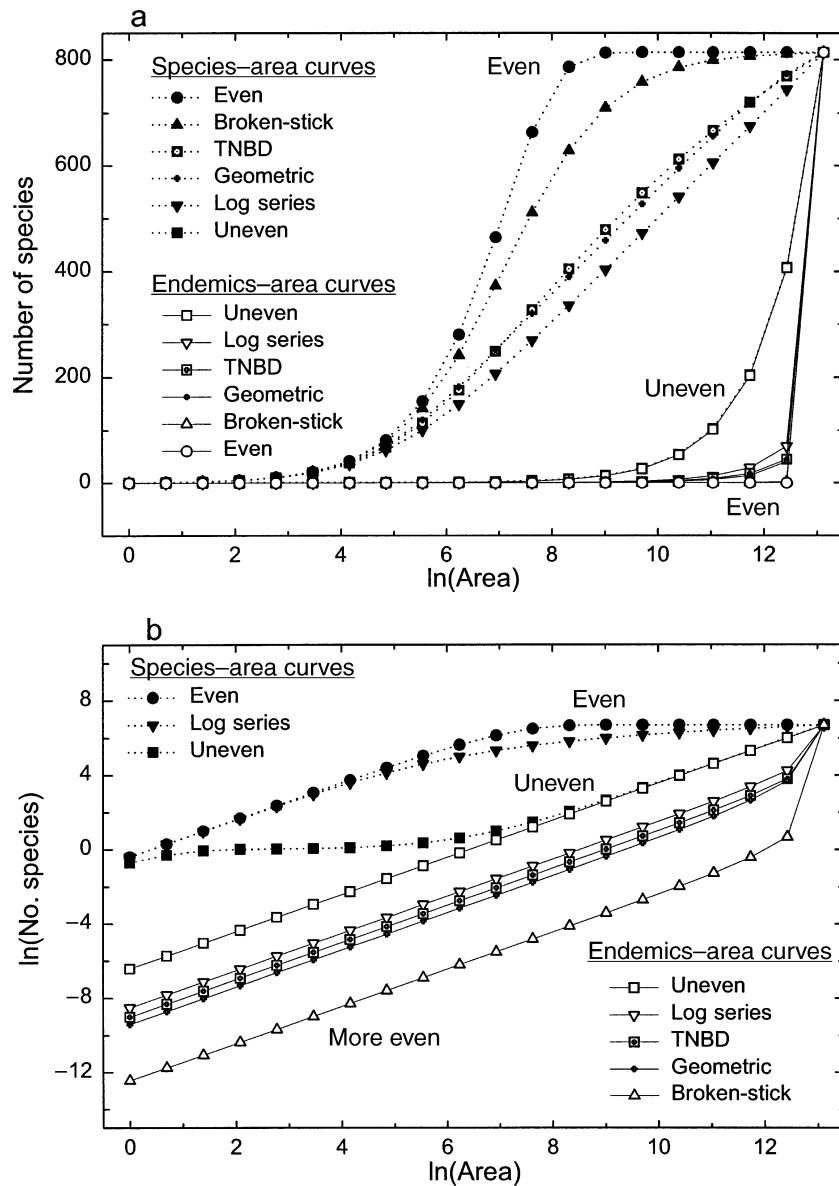
Fig. 1.   Endemics–area curves (open symbols) and species–area curves (closed symbols) of random placement for the species-abundance models in Table 1, fit to the Pasoh Forest species-abundance data. In contrast to the species richness pattern, endemic species diversity in a given sampling area increases with decreasing evenness. (a) The number of endemic species and species plotted against the natural logarithm of area (measured in square meters). (b) The natural logarithm of endemic and total species richness is plotted against the natural logarithm of area (measured in square meters), illustrating the difference between curves that appear to be nearly overlapping in (a). The endemic species richness for the even abundance distribution was zero at every spatial scale except for the largest; hence, the natural logarithm of the endemic species richness was not plotted for this distribution.

binomial distribution (NBD) is often used to model the spatial aggregation of individuals in biology, the en-demics–area relationship represented by Eq. 4, for pos-itive values of k_i, is not equivalent to an endemics–area relationship derived from the NBD. The NBD, unlike the random distribution model used in this analysis, is meant to capture the characteristics of a species dis-tribution only for small subregions x of a much larger region of size A, i.e., for $x \ll A$. It does not accurately capture the properties of nonrandom species distribu-tions in subregions of size $x \sim A$. In particular, it assigns a probability less than 1 for the species to be in a sample
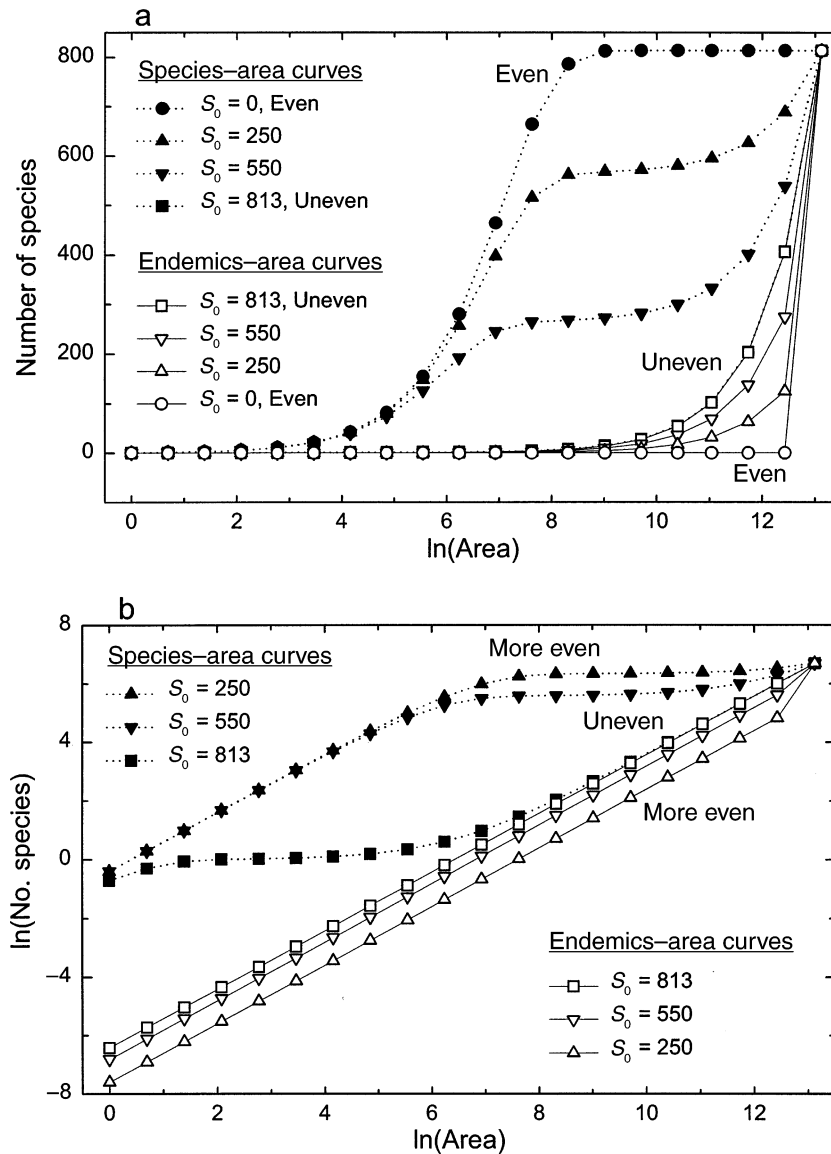
FIG. 2. Endemics–area curves (open symbols) and species–area curves (closed symbols) of random placement for different S_0. We assumed that study area $A = 500\,000$ m², total species richness $S = 814$, and total abundance $N = 335\,356$. The term S_0 denotes the number of species with one individual, and the remaining $N - S_0$ individuals are split equally among the remaining $S - S_0$ species. Lower values of S_0 result in more even species-abundance distributions. In contrast to the species richness pattern, endemic species diversity in a given sampling area decreases with increasing evenness (and decreasing S_0). (a) Endemic and total species richness plotted against the natural logarithm of area (measured in m²). (b) The natural logarithm of endemic and total species richness plotted against the natural logarithm of area (measured in m²).

of size A, which encompasses the whole region in which the species is known to be present. The factor $1 - x/A$ in Eq. 2, introduced by He and Legendre (2002), compensates for this, by forcing $p_i(A)$ to 1, but may not yield an accurate representation of the properties of a particular type of spatial aggregation well described by the negative binomial when $x \ll A$. However, as He and Gaston (2000) suggest, for $k_i \in (-\infty, -N_i x/A)$ and for $k_i \in (0, \infty)$, Eq. 2 models the probability of presence for an entire spectrum of spatial patterns, from regular to random to aggregated. We can thus apply Eq. 2 to explore the form of species–area relationships and endemics–area relationships for a spectrum of spatial and species-abundance distributions.

Effect of spatial distributions on endemic species richness

For any species-abundance distribution defined for the S species present in A, the effect of the spatial distribution on endemic species richness can be evaluated by varying the parameter k_i in Eq. 4. One would expect that more clustered spatial distributions would result in higher endemic species richness at a given subregion a. To explore this idea numerically, and to compare the endemics–area relationship to the species–area relationship as analyzed by He and Legendre (2002), we defined, as they did, $k_i = cN_ix/A$, where c is a constant scaling factor across all species. Fig. 3 compares the endemics– and species–area curves for different values of c ranging from negative (regular distribution) to positive (aggregated). For this example, we assumed a geometric series distribution fit to the Pasoh Forest species-abundance data (total species richness (S) = 814, total abundance across all species (N) = 335 356, and resource preemption parameter (K) = 0.009927). These curves show that, as expected, endemic species richness in a subregion a consistently increases with the intensity of spatial aggregation of the species, supporting the hypothesis that spatial regularity decreases endemic species richness in a subregion. This pattern is the opposite of what is seen for total species richness, which decreases with the intensity of spatial aggregation. When species are highly aggregated ($c = 0.0001$), the form of the endemics–area curve approaches that of the species–area curve. As species become less aggregated, total species richness increases with area much more rapidly than does endemic species richness. Finally, when the spatial distribution of species is highly regular ($c = -1.0001$), species are distributed everywhere throughout the larger region A, and hence are no longer confined (or endemic) to the smaller subregions within A.

DISCUSSION

In this paper, we have shown that an increase in regional-scale dominance and conspecific aggregation will result in an increased number of species endemic to a subregion. In particular, we have shown that these patterns hold in numerical examples in which we have separately varied dominance and aggregation. In addition to the examples documented in this paper, we performed simulations to evaluate the ''factorial'' effects of dominance combined with spatial distribution. For different combinations of dominance × spatial distribution, we always found that regional-scale dominance and conspecific aggregation increased endemism in a subregion.

The species present in an area consist of two groups: species that are endemic to that area and those with a range extending outside of that area. He and Legendre (2002) found that regional-scale dominance and conspecific aggregation both act to decrease the total number of species in a subregion. Combining our results with those of He and Legendre, we can infer that dominance and spatial aggregation will act to decrease the expected number of species in an area with a range extending outside that area.

In a recent theoretical paper, Plotkin and Muller-Landau (2002) found that conspecific aggregation decreases the expected number of species in common to two plots randomly sampled from a larger region. This result is consistent with our finding that conspecific aggregation increases the expected number of species endemic to a sampling area. As endemicity within plots increases, similarity between plots must decrease. Plotkin and Muller-Landau also solved for the expected similarity between two sampling areas assuming a range of different species-abundance distributions at the landscape scale, but did not explicitly investigate how the relative evenness or dominance of the species-abundance distribution impacts beta diversity. Our results suggest that increased dominance will decrease the expected fraction of species in common to two plots.

Our models and findings are of practical interest to conservation planning. The need to investigate the effect of spatial scale on risk assessments in a set of geographically nested areas is becoming widely recognized (Gärdenfors 2001). The models used in this study offer a quantitative tool to these investigations, enabling one to consider the impact of scale on endemic species richness in a wide range of circumstances. Furthermore, scaling patterns of endemicity can be applied to estimate the risk of extinctions following habitat loss due to deforestation (Kinzig and Harte 2000, Zurlini et al. 2002) or species range shifts induced by global warming (Green et al. 2001). Although there have been some empirical studies on the endemics–area relationship (Major 1988, Anderson 1994, Ceballos and Brown 1995, Harte and Kinzig 1997, Willerslev et al. 2002, Yeates et al. 2002, Zurlini et al. 2002), they are few in number, and hence these models may be particularly useful for making estimates for a range of scenarios in the absence of empirical guidance. Note that our results apply to two potentially useful definitions of endemism: global endemism and local endemism. Scaling patterns of global endemism are relevant to large-scale conservation planning and species extinction estimates. Scaling patterns of local endemism are relevant when considering local species extinctions, or population extinctions, which have been deemed an equal if not more sensitive indicator of the loss of biological capital than global species extinctions (Smith et al. 1991, Ceballos and Ehrlich 2002).
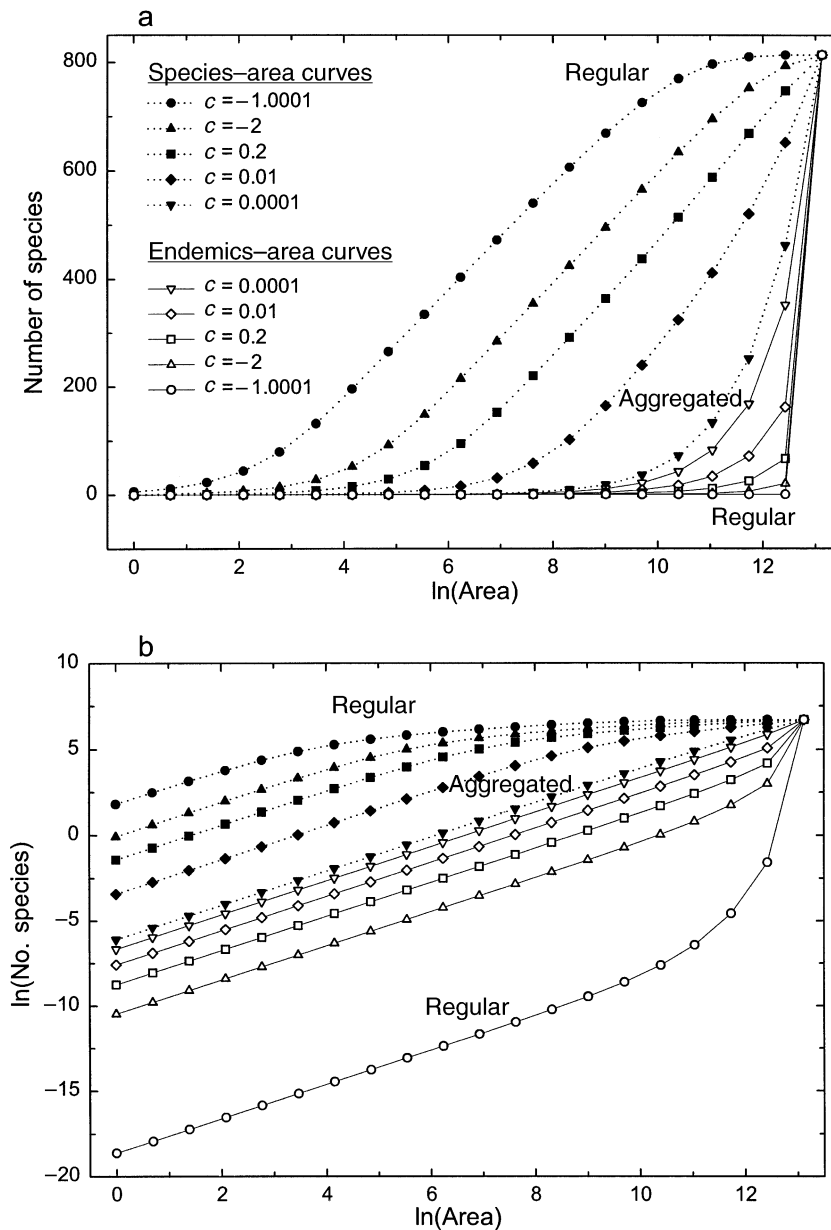
FIG. 3. Species–area curves of Eq. 3 (closed symbols) and endemics–area curves of Eq. 4 (open symbols) for different values of the scaling factor c. From $c = -1.0001$ (top and bottom curves) to $c = -2$, the spatial distribution of species shift from regular to random, whereas from $c = 0.0001$ (central curves) to $c = 0.2$, the spatial distributions shift from aggregated to random. In contrast to the species richness pattern, the number of endemic species in a given sampling area increases in spatial aggregation of the species. (a) The number of endemic species and total species plotted against the natural logarithm of area (measured in m²). (b) The natural logarithm of the number of endemic species and total species plotted against the natural logarithm of area (measured in m²).

In light of their results on the effect of dominance and spatial aggregation on species richness, He and Legendre (2002) proposed a hierarchical model for considering the effects of biotic and abiotic factors on species richness. In particular, they proposed that one

way to glean the potential effect of such factors on species richness is to consider their effects on species abundances and conspecific aggregation. We suggest that this hierarchical model is equally useful for considering the effects of biotic and abiotic factors on

endemic species richness. For example, the invasion of exotic species might cause an increase in regional-scale dominance, and hence increase the level of endemic species richness in subregions. An interesting consequence of our study is that biotic and abiotic factors that decrease dominance and conspecific aggregation will tend to increase the total species richness of a subregion, but decrease its endemic species richness. This could lead to negative correlations between endemic species richness and total species richness, as long as regional total and endemic diversity are held constant. Furthermore, under this hierarchical model, our results suggest that biotic or abiotic forces contributing to regional-scale species dominance and conspecific clustering may increase the risk of extinctions under habitat loss.

LITERATURE CITED

Anderson, S. 1994. Area and endemism. Quarterly Review of Biology **69**:451–471.

Bibby, C. J., N. J. Collar, M. J. Crosby, M. F. Heath, C. Imboden, T. H. Johnson, A. J. Long, A. J. Stattersfield, and S. J. Thirgood. 1992. Putting biodiversity on the map: priority areas for global conservation. International Council for Bird Preservation, Cambridge, UK.

Ceballos, G., and J. H. Brown. 1995. Global pattern of mammalian diversity, endemism, and endangerment. Conservation Biology **9**:559–568.

Ceballos, G., and P. R. Ehrlich. 2002. Mammal population losses and the extinction crisis. Science **296**:904–907.

Crisp, M. D., S. Laffan, H. P. Linder, and A. Monro. 2001. Endemism in the Australian flora. Journal of Biogeography **28**:183–198.

Gärdenfors, U. 2001. Classifying threatened species at national versus global levels. Trends in Ecology and Evolution **16**:511–516.

Green, J. L., J. Harte, and A. Ostling. 2001. Global warming, temperature homogenization and species extinction. Pages 179–199 *in* J. L. Lockwood and M. L. McKinney, editors. Biotic homogenization. Kluwer Academic/Plenum Publishers, New York, New York, USA.

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., A. Kinzig, and J. Green. 1999. Self-similarity in the distribution and abundance of species. Science **284**:334–336.

He, F., and K. J. Gaston, 2000. Estimating species abundance from occurrence. American Naturalist **156**:553–559.

He, F., and P. Legendre. 2002. Species diversity patterns derived from species–area models. Ecology **83**:1185–1198.

Kinzig, A. P., and J. Harte. 2000. Implications of endemics–area relationships for estimates of species extinctions. Ecology **81**:3305–3311.

Major, J. 1988. Endemism: a botanical perspective. Pages 117–146 *in* N. Myers and P. S. Giller, editors. Analytical biogeography. Chapman and Hall, New York, New York, USA.

Mittermeier, R. A., N. Myers, J. B. Thomsen, G. A. B. da Fonseca, and S. Olivieri. 1998. Biodiversity hotspots and major tropical wilderness areas: approaches to setting conservation priorities. Conservation Biology **12**:516–520.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature **403**:853–858.

Peterson, A. T., and D. M. Watson. 1998. Problems with areal definitions of endemism: the effects of spatial scaling. Diversity and Distributions **4**:189–194.

Pielou, E. C. 1975. Ecological diversity. John Wiley, New York, New York, USA.

Plotkin, J. B., and H. C. Muller-Landau. 2002. Sampling the species composition of a landscape. Ecology **83**:3344–3356.

Smith, T. B., S. Kark, C. J. Scheider, R. K. Wayne, and C. Moritz. 1991. Biodiversity hotspots and beyond: the need for preserving environmental transitions. Trends in Ecology and Evolution **16**:431.

Weiner, J., and O. T. Solbrig. 1984. The meaning and measurement of size hierarchies in plant populations. Oecologia **61**:334–336.

Willerslev, E., A. J. Hansen, K. K. Nielson, and H. Adsersen. 2002. Number of endemic and native plant species in the Gálapagos Archipelago in relation to geographical parameters. Ecography **25**:109–119.

Yeates, D. K., P. Bouchard, and G. B. Monteith. 2002. Patterns and levels of endemism in the Australian Wet Tropics rainforest: evidence from flightless insects. Invertebrate Systematics **16**:605–619.

Zurlini, G., L. Grossi, and O. Rossi. 2002. Spatial-accumulation pattern and extinction rates of Mediterranean flora as related to species confinement to habitats in preserves and larger areas. Conservation Biology **16**:948–963.