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SPECIES DIVERSITY PATTERNS DERIVED FROM SPECIES–AREA MODELS

FANGLIANG HE^{1,2,4} AND PIERRE LEGENDRE³

¹Canadian Forest Service, Pacific Forestry Centre, 506 West Burnside Road, Victoria, British Columbia, Canada V8Z 1M5

²Department of Statistics and Actuarial Science, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia, Canada V5A 1S6

³Département de sciences biologiques, Université de Montréal, C.P. 6128, succursale Centre-ville, Montréal, Québec, Canada H3C 3J7

Abstract. Although area, species abundances, spatial distribution, and species richness have been central components of community ecology, their interrelationships are not completely understood. To describe these interrelationships, we study and test three patterns regarding species richness using species–area models. The first one is the widely accepted generalization that states that the number of species monotonically increases with sampling area. The second pattern predicts the decrease in species richness with the increase of species dominance in a given area. The third one predicts that spatial aggregation of individuals within species results in lower species richness in communities. These three generalizations were investigated by modeling and simulations. First, a random-placement species–area model was used to evaluate the effects of relative species abundances on species richness in a sampling area. Then, a nonrandom species–area model was derived which explicitly encompasses the spatial distributions of species; it served to evaluate the effects of heterogeneity in spatial distributions on species richness. Species–area models were numerically evaluated using parameters estimated from a tropical rain forest community, and simulations were conducted to support the numerical solutions. The three patterns regarding species diversity were consistently supported by the results. A discussion ensues, describing how the three patterns can be used to interpret and predict species diversity, and how they are supported by other diversity hypotheses. The three generalizations suggest that, if we want to understand species diversity, we should go and look for mechanisms that influence the abundances and spatial distributions of species. If a mechanism can make the species abundances more even, or their spatial distributions more regular, this factor likely contributes to species coexistence.

Key words: abundance; aggregation; community ecology; dominance; evenness; random placement; scale; spatial distribution; species–abundance model; species–area; species diversity; species richness.

INTRODUCTION

Species richness, species relative abundances, and heterogeneity of their spatial or temporal distributions in a given area are the central subjects of community ecology. Ecologists have spent much effort and imagination to establish and quantify interrelationships among these components, and to identify the underlying biological or physical processes that influence them, e.g., extinction, immigration, colonization, niche segregation, competition, predation (Arrhenius 1921,

Paine 1966, MacArthur and Wilson 1967, Simberloff and Wilson 1969, Janzen 1970, Connell 1971, Connor and McCoy 1979, Gilpin and Diamond 1981, Tilman 1982, Rosenzweig 1996), environmental control (Whittaker 1956, Bray and Curtis 1957, Hutchinson 1957), disturbances, and historical dynamics (Levin and Paine 1974, Hubbell 1979, Sousa 1979, Hubbell and Foster 1986). On the one hand, a given model may suggest an ecological explanation for an observed phenomenon. For instance, population growth models may suggest that a population is under resource-unlimited (exponential model) or resource-limited growth (logistic model; Cui and Lawson 1982). On the other hand, confirmation of an assumed ecological process, or one

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⁴ E-mail: fhe@pfc.forestry.ca

found to be statistically significant, may help formulate a new model. An example of the latter case is the theory of island biogeography, which helps us model species diversity at both the local and regional scales (Wu and Vankat 1991). No doubt, this interactive procedure has greatly enhanced our understanding of how communities are organized, and therefore increased the accuracy of predictions of how communities change.

One of the most successful predictions in community ecology is that the number of species increases with sampling area. This species–area relationship is one of the most robust generalizations in ecology (Holt et al. 1999) and has been considered for a long time to be a “genuine law” of ecology (Schoener 1976); we will refer to it as the first pattern or generalization of species diversity. Another widely recognized relation, based largely on empirical observations, is that species richness decreases with the increase of species dominance in a given area, i.e., with the increase in unevenness in species abundances (Bazzaz 1975, Huston 1979, Armesto and Pickett 1985, Crawley 1997). We may call this species–dominance relationship the second pattern of species diversity. Furthermore, ecologists have found that species richness in an area greatly depends on the distributional patterns of species (Williams 1943, Janzen 1970, Connell 1971, Crawley 1997, Ney-Nifle and Mangel 1999); little generality has been achieved along this line, however. As a hypothesis, we are now proposing a third pattern of species diversity, which predicts higher species richness in a sampling area if the species are spatially more regularly distributed in the community. This species–aggregation relationship thus predicts that spatial aggregation of individuals within species results in lower species richness in a study area.

The species–area relationship is widely accepted in community ecology. The species–dominance and species–aggregation relationships, however, have not been subjected to much analytical or numerical scrutiny, although some solutions have been explored by Crawley (1997). The purpose of this paper is to evaluate and generalize the effects of dominance and spatial aggregation (clumping, patchiness) on the number of species in a given area. Although ecologists are still struggling to understand the effect of area (Begon et al. 1996), we know much less about the effects of dominance and spatial aggregation on the number of species encountered in an area. This may be due in large part to the difficulty of modeling species dominance and spatial aggregation of species.

In this study, species diversity (or diversity) is exchangeably used with species richness (or the number of species), as in several recent papers (e.g., Abrams 1995, Tilman 1999). The study is organized as follows. First, from the principles of sampling theory, we introduce the species–area model for species with random spatial arrangement of individuals. Based on this model, several species–area models for different values of

species evenness are derived; they describe the effects of various degrees of dominance on the species richness of a community. Second, a species–area model for nonrandom distribution of individuals is derived based on a probabilistic model for species presence, by which the effect of spatial heterogeneity in the distribution of individuals can be evaluated. Third, the random placement and nonrandom species–area models are numerically estimated to show the effects of dominance and spatial aggregation on species richness, using an empirical data set from a tropical rain forest. In that section, simulations are also conducted to support the numerical results for the effects of aggregation and dominance on species richness. A discussion follows which describes how the three patterns can be used to interpret and predict species diversity and how the patterns are supported by other diversity hypotheses.

SPECIES–AREA MODELS UNDER RANDOM DISTRIBUTION

A species–area model for species with random distribution of individuals in a fixed-size area A was derived by Arrhenius (1921) and Coleman (1981). In a given study area A , assume there are S species with abundances $\{N_i, i = 1, 2, \dots, S\}$. If the N_i individuals of species i are randomly distributed through A , the probability of finding a particular individual of the species in a sampling area a is a/A . Therefore, the number of individuals, n_i , of the species in area a follows a binomial distribution:

$$p(n_i|a) = \binom{N_i}{n_i} \left(\frac{a}{A}\right)^{n_i} \left(1 - \frac{a}{A}\right)^{N_i - n_i},$$

for $n_i = 0, 1, 2, \dots, N_i$.

When $n_i = 0$, it means that no individual of species i occurs in sampling area a ; the probability of absence for the species is thus $(1 - a/A)^{N_i}$. In contrast, the probability of presence of the species is $1 - (1 - a/A)^{N_i}$. The presence or absence of a species in area a is obviously a Bernoulli trial. Therefore, the expected number of species, s_a , in a is the sum of the independent but nonidentical Bernoulli trials for species $i = 1, 2, \dots, S$, which leads to the species–area model for random placement:

$$s_a = S - \sum_{i=1}^S \left(1 - \frac{a}{A}\right)^{N_i}. \quad (1)$$

Eq. 1 implies that for species that are homogeneously and randomly distributed through space, the number of species in sampling area a is solely determined by species abundances $\{N_i\}$ of the community, suggesting that different species–abundance distributions will give rise to different numbers of species in area a .

For a community with total abundance $N = \sum_{i=1}^S N_i$, the species abundances $\{N_i, i = 1, 2, \dots, S\}$ can be divided in many different ways among the S species, ranging from the most even $\{N_i = N/S, i = 1, 2, \dots,$

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

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

Notes: The species–area curves were derived by inserting the different species-abundance models into Eq. 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, s_a is the number of species in sampling area a . Geometric series: n_i is the number of individuals of the i th species for $i = 1, 2, \dots, S$; K is the resource pre-emption parameter. Truncated negative binomial distribution (TNBD): γ is the shape parameter measuring the shape of the species-abundance distribution, ϕ is the scale parameter. Log-series distribution: α and x are parameters.

S to the most uneven distribution $\{N_i = 1 \text{ for the first } S-1 \text{ species, and } N_S = N - S + 1 \text{ for the } S\text{th species}\}$. Several species-abundance models may be used to describe the intermediate situations, although only discrete models are included in this study because our data consist of numbers of individuals. A further criterion to select a species-abundance model is that the fitted model must satisfy the condition that the sum of the estimated abundances for the S species equals N , by which we ensure that the total abundance (N) is really distributed among the S species in a way comparable with the given community $\{N_i, i = 1, 2, \dots, S\}$. Despite its wide use in ecology, the lognormal distribution satisfies neither criterion and was therefore excluded from the present study. The species-abundance models used in the present study and their corresponding species–area curves are given in Table 1. The derivation of the random placement species–area curves is straightforward. The species–area curves for the log series and broken-stick models were initially given by Coleman (1981). For the purposes of illustration, we now give the derivation of the species–area curves for the uneven and log-series models of Table 1.

The most uneven species-abundance model is that where each of the first $S-1$ species is represented by only one individual whereas the S th species has $N-S+1$ individuals. Substituting these abundances into Eq. 1 gives

$$s_a = S - \sum_{i=1}^{S-1} \left(1 - \frac{a}{A} \right)^1 - \left(1 - \frac{a}{A} \right)^{N-S+1}$$

which simplifies to the formula in Table 1. Similarly, for the log-series model, we know there are αx species with one individuals, $\alpha x^2/2$ species with two individuals, \dots , $\alpha x^n/n$ species with n individuals, etc. Substituting these terms into Eq. 1 gives

$$s_a = S - \alpha x \left(1 - \frac{a}{A} \right) - \alpha \frac{x^2}{2} \left(1 - \frac{a}{A} \right)^2 - \dots - \alpha \frac{x^n}{n} \left(1 - \frac{a}{A} \right)^n - \dots$$

A summation over the series leads to the species–area curve for the log-series model in Table 1. Other species–area models in Table 1 are likewise derived.

A critical concern for evaluating the effect of dominance (complement of evenness) on species–area curves is the measure of evenness. There are about a dozen evenness indices available in the literature (Smith and Wilson 1996, Kokko et al. 1999). Different indices emphasize different aspects of dominance (e.g., rare vs. common species), and they may not be monotonic to one another. We used two indices to measure evenness in abundances: Pielou's evenness J' and Gini's coefficient g . The former, the most widely used in ecology, is expressed by the Shannon information scaled by the maximum information (Pielou 1975); J' ranges from 1 to 0, representing changes in distribution of abundances from even to uneven. The latter is traditionally used to measure income inequality or inequality in plant sizes (Damgaard and Weiner 2000); it was calculated using the formula given by Johnson et al. (1994); g ranges from 0 to 1 and represents chang-

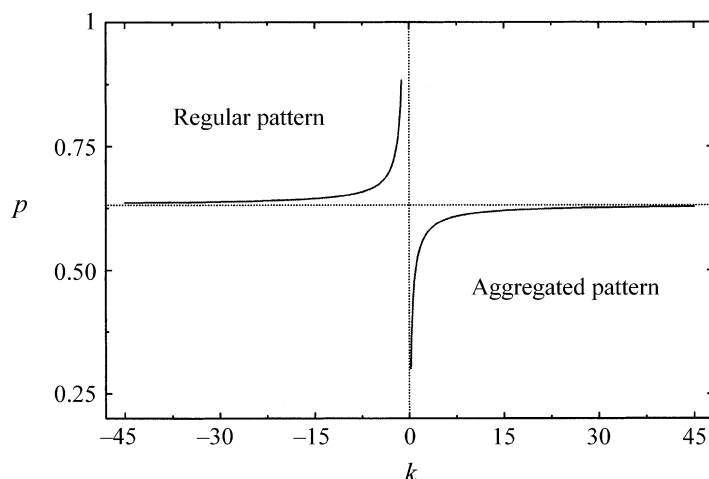


FIG. 1. Probability p of presence (Eq. 4) illustrating how p changes with k for $\mu = 1.0$. When $k \rightarrow \pm\infty$ in opposite directions (from aggregated on the positive side of the abscissa or from regular on the negative side), the spatial distribution of the species converges to random (i.e., Poisson distribution) in which the expected probability of presence is $1 - e^{-\mu}$, resulting in $p = 0.632$ for $\mu = 1.0$.

es in distribution of abundances from even to uneven. There is no guarantee, however, that these two indices will give consistent results across all abundance models of Table 1 because these models differ in skewness and kurtosis. This situation raises a difficulty in interpreting the effect of evenness on species–area models. To obtain an unambiguous evaluation, we must use a series of data sets that represent a monotonic change in evenness. Two particular data generation models have this property.

The first one is that where the total abundance N is divided in such a way that each of the first S_0 species has only one individual while the remaining individuals (i.e., $N - S_0$) are split equally among the remaining $S - S_0$ species. The random placement species–area curve for this model is

$$s_a = S_0 \frac{a}{A} + (S - S_0) \left[1 - \left(1 - \frac{a}{A} \right)^{(N-S_0)/(S-S_0)} \right]. \quad (2)$$

When $S_0 = 0$, Eq. 2 is the most even model in Table 1, while if $S_0 = S - 1$ it is the most uneven model. Evenness strictly decreases when S_0 changes from 0 to $S - 1$. The effect of evenness on species–area curves is unambiguous using this model.

The second data generation model is the truncated negative binomial distribution (TNBD) in which evenness in abundances is determined by the shape parameter γ (Pielou 1975). Evenness strictly decreases with decreasing γ . The TNBD and its random placement species–area equation are given in Table 1. Given the total abundance N and the total number of species S of a community, γ and ϕ (scale parameter) follow the relationship

$$\frac{\gamma\phi}{1 - (1 + \phi)^{-\gamma}} = \frac{N}{S}. \quad (3)$$

By varying γ and the corresponding ϕ (holding N and S constant), we can unambiguously evaluate the effect of evenness on species–area models.

SPECIES–AREA MODELS UNDER NONRANDOM DISTRIBUTION

In nature, individuals of most species are seldom randomly distributed through space (He et al. 1997, Condit et al. 2000). Departing from randomness, spatial distributions may be regular or aggregated, the latter being typically observed (Taylor et al. 1978, Greig-Smith 1983). If a species is aggregated, the probability of presence of the species in a sampling area a should be less than that under random distribution, and the higher the aggregation, the smaller the probability of presence. Conversely, if a species has a regular distribution, the probability of presence of the species in a should be larger than in the random case, and the more regular, the higher the probability. He and Gaston (2000) showed the probability of presence for a species with abundance N_i to be

$$p_i = 1 - \left(1 + \frac{N_i a}{A k} \right)^{-k} \quad (4)$$

where k is a parameter varying in the intervals $(-\infty, -\mu_i)$ and $(0, \infty)$ which describes the spatial pattern of the species, and $\mu_i = N_i a / A$ is the mean density of the species in area a . When k is positive, Eq. 4 represents the probability of presence for species i derived from a negative binomial distribution; a smaller value of k describes stronger spatial aggregation (He and Gaston 2000). When k is negative, Eq. 4 represents the probability of presence for species i derived from a binomial distribution, describing regular spatial distribution (Greig-Smith 1983). When $k \rightarrow -\mu_i$ from the negative side, regularity becomes maximum. When $k \rightarrow \pm\infty$, the spatial distribution converges to random (the Poisson distribution) but from different directions: regular to random on the left, and aggregated to random on the right (Fig. 1).

In the regular case, an upper bound for regularity is naturally imposed by the ceiling in number of points

(trees) distributed in the area, given the fact that adjacent trees must keep to some minimum distance. To pack more trees in the area, the minimum distance between trees must be reduced. This suggests that for a given number of trees, the parameter k in Eq. 4 cannot be as large as one may wish; k has the constraint $k \leq -\mu_i$.

By common sense, when sampling area $a = 0$, the probability of presence equals 0, whereas if $a = A$, the probability of presence equals 1 (when the whole plot is covered, one is certain that species i has been sampled). Eq. 4 does not satisfy the latter condition. A simple modification can be made to Eq. 4 to reflect this:

$$p_i = 1 - \left(1 - \frac{a}{A}\right) \left(1 + \frac{N_i a}{A k_i}\right)^{-k_i} \quad (5)$$

The qualitative behavior of this probability function is the same as that of Eq. 4.

As for Eq. 1, we can now write the equation of a species–area model for nonrandom spatial distributions of species in terms of Eq. 5 for a community having a total number of S species with abundances $\{N_i, i = 1, 2, \dots, S\}$ (Note: a similar “collector’s curve” is given by Pielou 1975)

$$s_a = S - \left(1 - \frac{a}{A}\right) \sum_{i=1}^S \left(1 + \frac{N_i a}{A k_i}\right)^{-k_i} \quad (6)$$

where k_i is a parameter describing the spatial distribution of species i . When $a = 0$, $s_a = 0$; when $a = A$, $s_a = S$. Furthermore, when all $k_i = -\mu_i$ ($= -N_i a / A$), the species are so regularly distributed that every species is almost certainly present in a sampling area a , resulting in $s_a = S$.

Compared to Eq. 1, Eq. 6 encompasses both the information about species abundance (N_i) and their spatial distribution (k_i) into the species–area relation. Therefore, for any species–abundance model such as those in the left-hand column of Table 1, and given a value k_i for each species i , the effect of spatial distribution on species–area relations can be evaluated. However, k_i is not a constant for a population; its value depends on the size of the sampling area and on the population density (Anscombe 1949, Taylor et al. 1979). To estimate a particular value k for a given area is not our objective here; our purpose is to show how species richness in Eq. 6 changes with the change in spatial distribution realized by changing k systematically (e.g., from low to high values). Without loss of generality, we can define $k_i = c\mu_i$, where c is a constant scaling factor across all species that converts density into a k_i value. A negative c leads to a regular spatial distributions whereas a positive c produces an aggregated pattern. A species achieves maximum regularity when $c \rightarrow -1^-$, and it is highly aggregated when $c \rightarrow 0^+$. Therefore, for any given species–abundance data or model, the effect of spatial distribution on s_a in Eq. 6

can be evaluated by changing c from negative to positive.

NUMERICAL EVALUATION

The data

Although Eqs. 1 and 6 combine area (a), abundance (N_i), spatial distribution (k_i), and number of species (s_a), examination of these equations, and of those in Table 1, does not tell us how these parameters numerically affect one another. In particular, we do not know if the second and third patterns hypothesized in the introduction hold, i.e., whether dominance in abundance or aggregation in space really reduce species richness in an area. To answer these questions, it is necessary to conduct numerical evaluations, ideally using real data containing complete information about abundances and spatial distributions of all species occurring in the community. Such data sets are rare, but we were fortunate enough to have access to one. Using these data, we kept the total number of species and the total abundance of individuals fixed, but allowed the total abundance to be distributed in various ways among the species, from even to uneven, to evaluate the effect of dominance (Eq. 1). We also allowed the spatial distributions of species to vary when evaluating the effect of spatial patterns (Eq. 6). In this way, we avoided confounding the effect of total number of species and total abundance on the species–area models.

The community is from a lowland tropical rain forest located in the Pasoh Forest Reserve of Malaysia (hereafter called the Pasoh Forest; Manokaran et al. 1999). The study area is a 500×1000 -m rectangular plot. The plot was initially set up and surveyed in 1987. The census was repeated in 1990 and 1995. In each survey, all free-standing trees and shrubs ≥ 1 cm diameter at breast height were enumerated, positioned by geographic coordinates on a reference map, and identified to species. In the 1987 survey, there were 335 356 stems belonging to 814 species, i.e., $N = 335\,356$ and $S = 814$. The most abundant species had 8962 individuals. Most of the species (80.4%) were aggregated, 19.5% had random spatial distributions, and one had a regular distribution (He et al. 1997). The species–area relationship for this plot has been reported by He and Legendre (1996). Unless explicitly mentioned, the data from the 1987 census are used in the following analyses.

Effect of species dominance on species richness

To evaluate the effect of dominance on the species–area curve, we will vary only the dominance parameter; by assuming that all species have random spatial distributions. The simplest model for random distribution is Eq. 1. Based on the species–abundance distribution observed in the Pasoh Forest, $\{N_i, i = 1, 2, \dots, 814\}$, we can create many “communities” by holding the number of species unchanged ($S = 814$) but varying

TABLE 2. Estimated parameters (left-hand column) for each species-abundance model in Table 1 using the Pasoh Forest species-abundance data, assuming random spatial distribution of individuals for each species.

Species-abundance models	J'	g
Most even: $n_1 = n_2 = \dots = n_{813} = n_{814} = 335356/814$	1	0
Broken-stick: $S = 814$, $N = 335356$	0.937	0.492
Observed species abundances	0.843	0.722
Geometric: $K = 0.009927$	0.836	0.755
TNBD: $\gamma = 0.1363$, $\phi = 1945.9970$	0.824	0.694
Log series: $\alpha = 100.3014$, $x = 0.999701$	0.774	0.729
Most uneven: $n_1 = n_2 = \dots = n_{813} = 1$, $n_{814} = 334543$	0.005	0.998

Notes: The dominance in species abundance for each model was measured by Pielou's evenness J' and Gini's coefficient g . The models are ordered by decreasing values of J' . The two measures of evenness are not monotonic. "Most even" and "most uneven" refer to hypothetical models by assuming two extreme species abundance distributions for the 335 356 trees among the 814 species in the Pasoh plot. "Observed species abundances" gives evenness for the observed abundances of the 814 species in the Pasoh forest; the others are fitted models.

the distribution of abundances among them for fixed N (=335 356). In one of these communities ("most even" in Table 2), all 814 species have equal abundances, or 411.985 individuals per species; this situation corresponds to $S_0 = 0$ in Eq. 2. At the other end of the spectrum is a community ("most uneven" in Table 2) in which each of the first 813 species has only one individual whereas the 814th species is represented by 334 543 individuals; this situation corresponds to $S_0 = 813$ in Eq. 2. Between these two extremes one finds the other models in the left-hand column of Table 1. A second possibility (Table 3) is to compute Eq. 2 for S_0 varying from 0 to 813. A third possibility (Table 4) is to compute the TNBD species-area model for different values of γ for the Pasoh data. After fitting each species-abundance model, the corresponding evenness indices were computed (Tables 2–4).

The species-abundance models in Table 1 were estimated by fitting them to the observed data. The parameter estimates so obtained (Table 2, left-hand column) were used in the corresponding species-area models. Parameter estimation for the broken-stick, geometric series, and log-series models followed the procedures summarized by Magurran (1988), whereas the moment method was used for TNBD (Pielou 1975). We

want to point out that, by estimating the parameters of species-abundance models, we are not suggesting that the Pasoh data can adequately be modeled by them. Modeling the species-abundance data of the Pasoh Forest is not our purpose; goodness of fit is not an issue here. All the parameterized species-abundance models in Table 1 satisfied the following conditions: (a) the sum of the estimated abundances in each model was equal to the observed total abundance (335 356 individuals) and (b) the total number of species was 814. Fig. 2a shows the species-area curves corresponding to the parameterized species-abundance models of Table 2.

The evenness measures for the species-abundance models in Table 2 show that indices J' and g are not monotonic to each other. This makes the interpretation of Fig. 2a difficult, although the species-area curves are very consistent with J' in that the number of species in a given area a increases with evenness measured by J' , except for the species-area curve for geometric series which crosses the TNBD curve. To avoid this ambiguity, we turned to Eq. 2 for different S_0 values and to the TNBD model for different γ values. In both

TABLE 3. Species-abundance models defined by assigning each of the first S_0 species to have one individual; the remaining individuals were divided equally among the other species.

Species abundance	J'	g
$S_0 = 0$ (most even)	1	0
$S_0 = 100$	0.981	0.123
$S_0 = 250$	0.946	0.306
$S_0 = 400$	0.900	0.491
$S_0 = 550$	0.834	0.674
$S_0 = 700$	0.709	0.858
$S_0 = 813$ (most uneven)	0.005	0.998

Notes: The estimated evenness for different values S_0 , using either Pielou's evenness J' or Gini's coefficient g , are monotonic in this case. The species-area model is given by Eq. 2 and shown in Fig. 2b.

TABLE 4. Species-abundance models defined by the TNBD (Table 1) for different values of parameter γ .

Species abundance	J'	g
Most even	1	0
$\gamma = 2$, $\phi = 205.9878$	0.966	0.373
$\gamma = 1$, $\phi = 410.9853$	0.937	0.492
$\gamma = 0.5$, $\phi = 794.7613$	0.896	0.595
$\gamma = 0.3$, $\phi = 1210.0497$	0.846	0.649
$\gamma = 0.1363$, $\phi = 1945.9970$	0.824	0.694
$\gamma = 0.01$, $\phi = 3193.8362$	0.778	0.727
Most uneven	0.005	0.998

Notes: Given a γ , ϕ is determined from Eq. 3 by holding $N = 335 356$ and $S = 814$ of the Pasoh forest. The "most even" and "most uneven" cases are the same as in Table 2. The estimated evenness for different γ , using either Pielou's evenness J' or Gini's coefficient g , are monotonic. The species-area model is given by the TNBD equation in Table 1 and shown in Fig. 2c.

cases, the J' and g measures are monotonic (Tables 3 and 4). The species–area curves for Eq. 2 and TNBD are shown in Fig. 2b and c, respectively. The relationships between species evenness and the species–area models are now convincingly shown: the number of species in a sampling area consistently increases with evenness whereas species dominance reduces species richness.

Effect of spatial distributions on species richness

Given a set of abundance data, the effect of the spatial distributions of species on richness can readily be evaluated using Eq. 6 by varying parameter k_i . The actual observed abundances of the 814 species in the Pasoh Forest were used in these evaluations. As shown above, the spatial distribution of species i ($i = 1, 2, \dots, 814$) is defined by $k_i = c\mu_i$, where $\mu_i = N_i a/A$ is the mean density of species i in a sampling area a , and c remains constant across all species. The species–area curves of Eq. 6 for values of c ranging from negative (regular distribution) to positive (aggregated) are shown in Fig. 3. The species–area curve for random pattern (not shown) is located between the curves for $c = -2$ and $c = 1$; the random-distribution model is obtained when $c \rightarrow \pm\infty$. These curves show that species richness in a sampling area a consistently decreases with the intensity of spatial aggregation of the species, as predicted by the hypothesis that spatial regularity of species distributions promotes species richness in a sampling area; in other words, spatial aggregation results in lower richness in a sampling area within a community.

Simulating the effect of spatial distribution on species richness

To further test the hypothesis stated in the third pattern of species diversity, we conducted additional simulations using the Pasoh data under the condition that the observed abundances of the 814 species remain unchanged, while the spatial distributions of all species were changed from highly regular to highly aggregated.

The regular scenarios were simulated using a simple sequential inhibition algorithm (Diggle 1983) with distance between conspecifics being at least $d_r/\sqrt{N_i}$ meters in the simulated pseudoforests, where N_i is the actual observed abundance of species i . In this study, three d_r values were used: 585, 300, and 0. According to Tanemura (1979) $d_r = 585$, which corresponds to a packing intensity of 0.538 for the most abundant species (=8962 stems), is nearly the most regular pattern attainable, whereas $d_r = 0$ corresponds to a random pattern.

The aggregated scenarios were simulated as follows: 814 points were randomly chosen on the Pasoh map; individuals of each of the 814 species were distributed around one of the generated points with radius at most $d_c N_i$ meters. Four d_c values were used: 1, 0.5, 0.01, and 0. Large d_c resulted in distributions tending towards

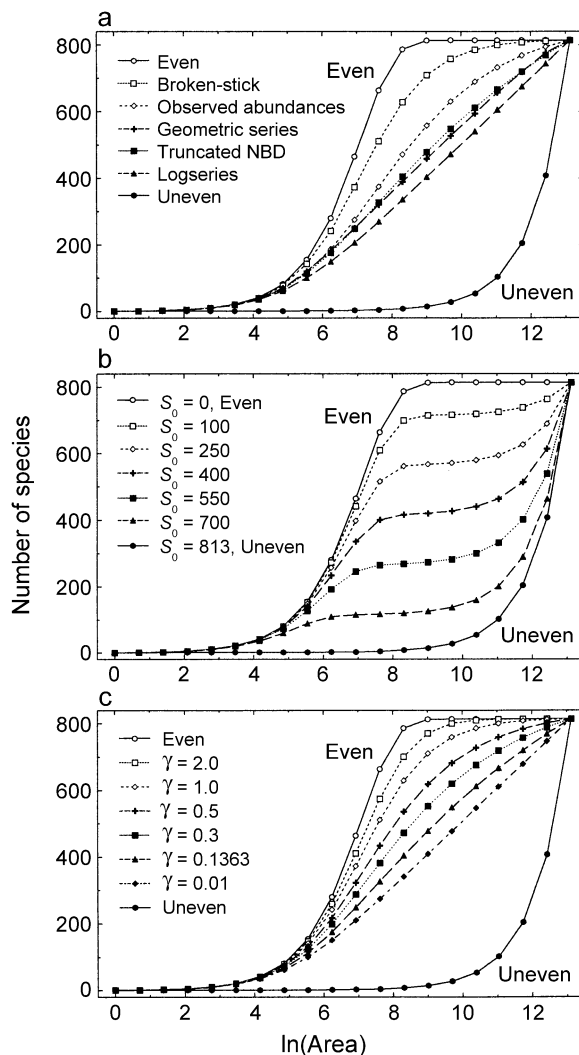


FIG. 2. Species–area curves of random placement showing the effect of species abundances. The number of species is plotted against the natural logarithm of area (in m^2): (a) species–area curves for the species-abundance models in Table 2; (b) species–area curves of Eq. 2 for different S_0 . The evenness in species abundances decreases with the increase of S_0 (Table 3), and so does the number of species in a given sampling area. (c) Species–area curves for the TNBD, with γ varying from 2.0 to 0.01 representing the decrease in evenness in the species abundances (Table 4). The number of species in an area decreases with decreasing evenness.

randomness whereas $d_c = 0$ represented an extreme pattern in which all individuals of a species were aggregated onto a single point.

For each simulation, species–area data were sampled by randomly locating, on the Pasoh map, quadrats belonging to 19 fixed sizes: 1×1 m (10 000 quadrats were sampled), 1×2 (10 000), 2×2 (5000), 2×4 (5000), 4×4 (2500), 4×8 (2500), 8×8 (2000), 8×16 (2000), 16×16 (1000), 16×32 (1000), 32×32 (512), 32×64 (256), 64×64 (128), 64×128 (64), 128×128 (32), 128×256 (16), 250×250 (8),

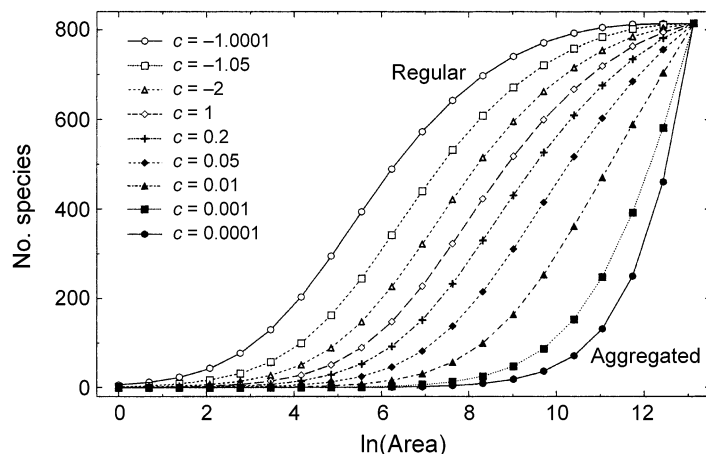


FIG. 3. Species-area curves of Eq. 6 for different values of the scaling factor c : number of species plotted against natural logarithm of area (in m^2). From $c = -1.0001$ (top curve) to $c = -2$, the spatial distributions of species shift from regular to random, while from $c = 0.0001$ (bottom curve) to $c = 1$, the spatial distributions shift from aggregated to random. The number of species in an area decreases with the increase in spatial aggregation of the species.

250 \times 500 (4), and 500 \times 500 (2). The mean number of species was calculated across the sampled quadrats for each quadrat size. The species-area curves for the different spatial distributions of species are shown in Fig. 4. The shapes of the species-area curves in Fig. 4 are not consistent from aggregated to regular. The inverse S-shape for $d_c = 0.5$ and 1 reflects the transition from the concave-up species-area curves for small d_c to the sigmoid curves obtained with more regular spatial patterns. Nevertheless, the simulation results support the analytical conclusions of the last section, i.e., the number of species in a sampling area increases with the regularity of the spatial distribution of the species, whereas spatial aggregation reduces species richness. We should point out, however, that this may not always occur with small sampling areas, e.g., $a \leq 16 \times 16$ m; in one instance, we found that the sampled number of species for an aggregated pattern was larger than observed for a less aggregated pattern. This phenomenon was also found in a simulation of incidence probability for a single species by Williams (1995, see his Fig. 2). It is not clear how this may happen but sampling error is a possible explanation.

Simulating effect of dominance and spatial distribution on species richness

So far, the effects of species dominance and spatial distribution were independently assessed. In the present section, we will use simulations to evaluate the "factorial" effects of dominance combined with spatial distribution. It is impractical to simulate species-area curves for each dominance \times distribution combination. Instead, we assessed the factorial effect by calculating the number of species in a fixed area (i.e., a 100 \times 100-m quadrat) for each combination of dominance \times spatial distribution.

In the simulation, the levels of dominance were kept the same as in Table 3 (see also Fig. 2b and Eq. 2) with $S_0 = 0, 100, 250, 400, 550, 700$, and 813, while changing the spatial distribution from strong regularity to strong aggregation with $d_r = 585, 300, 0$ to $d_c = 1, 0.5, 0.01$ as in Fig. 4. The number of species in each dominance \times distribution combination was averaged by randomly placing a 100 \times 100-m sampling quadrat 50 times onto the simulated Pasoh plot. The results in Table 5 show that the largest number of species occurs

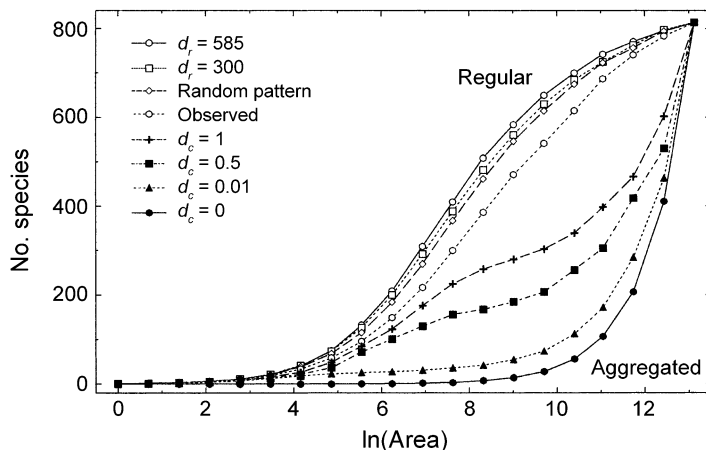


FIG. 4. Species-area curves sampled from the simulated spatial distributions for the 814 Pasoh species: number of species plotted against natural logarithm of area (in m^2). Larger d_r represents stronger spatial regularity while smaller d_c represents strong aggregation. The number of species in an area decreases with the increase in spatial aggregation of the species.

TABLE 5. The "factorial" effect of dominance \times spatial distribution on the number of species in the simulated Pasoh plot.

Dominance S_0	Spatial distribution					
	Strong regular ($d_r = 585$)	Intermediate regular ($d_r = 300$)	Random ($d_r = 0$)	Weak aggregated ($d_c = 1$)	Intermediate aggregated ($d_c = 0.5$)	Strong aggregated ($d_c = 0.01$)
0 (Most even)	814 (0.0)	814 (0.0)	813.9 (0.2)	544.8 (103.6)	297.2 (51.5)	18.9 (3.5)
100	716.1 (1.4)	716.0 (1.4)	715.6 (1.5)	538.0 (88.2)	290.1 (59.6)	18.8 (3.6)
250	569.6 (2.2)	569.4 (2.4)	568.8 (2.0)	483.9 (66.7)	296.5 (54.3)	18.9 (4.1)
400	422.5 (2.9)	422.0 (2.8)	422.8 (3.0)	414.5 (12.9)	290.3 (50.8)	18.7 (4.8)
550	275.2 (3.3)	274.9 (2.6)	274.3 (3.7)	274.9 (3.5)	244.3 (28.6)	18.8 (3.7)
700	128.9 (3.6)	129.0 (3.7)	128.4 (3.7)	127.3 (4.3)	128.1 (3.4)	18.7 (3.6)
813 (Most uneven)	18.0 (3.8)	17.4 (4.1)	17.5 (4.6)	17.4 (4.5)	16.6 (3.8)	16.2 (4.6)

Notes: The dominance treatment (S_0) is defined as in Table 3; the spatial distribution treatment (d_r , random, and d_c) is defined as in Fig. 4. In each dominance \times distribution simulation, a 100×100 -m sampling quadrat was randomly placed 50 times onto the plot. The number of species reported in the table was averaged from the 50 samples; the standard deviation is given in parentheses. For comparison, the mean number of species over 50 samples from the actual Pasoh plot is 491.3 with standard deviation = 24.6.

when species abundances are the most even ($S_0 = 0$) and distributions of species are the most regular ($d_r = 585$); species richness is lowest when abundances are the most uneven ($S_0 = 813$) and species are highly aggregated ($d_c = 0.01$). It is also clear from the results that the adverse impact of spatial aggregation on richness can be balanced out by increasing evenness, and vice versa.

The simulation results do not strictly monotonically change with the dominance levels and spatial distributions. For instance, the mean number of species for the combination $S_0 = 250$ and $d_c = 0.5$ is 296.5. This is slightly higher than 290.1 for the combination $S_0 = 100$ and $d_c = 0.5$. However, the difference falls within sampling variation.

DISCUSSION

Community ecology is sometimes described as a discipline lacking in general rules/laws, although ecology in general is not lacking in useful generalizations (Lawton 1999). This state of the discipline is, on the one hand, due to the entanglement of the interactions between abiotic and biotic factors at the scale of the community and beyond, and on the other hand, to the fact that ecologists seem powerless to disentangle them. The number of species in an area (or island) has been found to originate and be maintained by many factors, as mentioned in the *Introduction*. The fact that these factors interact and confound one another and that each factor varies across time and space makes the interpretation of species diversity data very difficult and controversial (e.g., Hamilton et al. 1963, Johnson and Raven 1973).

A hierarchical model to interpret species richness

To sort out these factors and facilitate interpretation, He and Legendre (1996) proposed that, at the community level, the abundances and spatial distributions of species are the two immediate components that directly determine a species–area relationship, while other factors or mechanisms are indirect yet ultimate in the sense that they affect species richness through their effects on the abundance and spatial distribution (Fig. 5). This fact is precisely reflected by the species–area models investigated in this study; they are all derived from Eqs. 1 and 6 in which species abundances and spatial distributions are the only two components explicitly included in the models. Compared with specific environmental or biotic explanations of diversity, the advantage of the three patterns studied in this paper is that they propose an interpretation of species diversity at a higher level than mechanistic processes (Fig. 5). For example, the third pattern predicts that spatial regularity can facilitate species coexistence, no matter that the observed regularity in spatial distributions is caused by the infestation of pathogens, the action of herbivores, or competition. The value of these generalizations is that they suggest a way of interpreting diversity patterns. If we want to understand species diversity, we should go and look for mechanisms that influence the abundances and spatial distributions of species. If a mechanism can make the species abundances more even, or their spatial distributions more regular, this factor should contribute to species coexistence, and vice versa. Abundance and spatial distribution are also considered by Crawley (1997) to be the two most im-

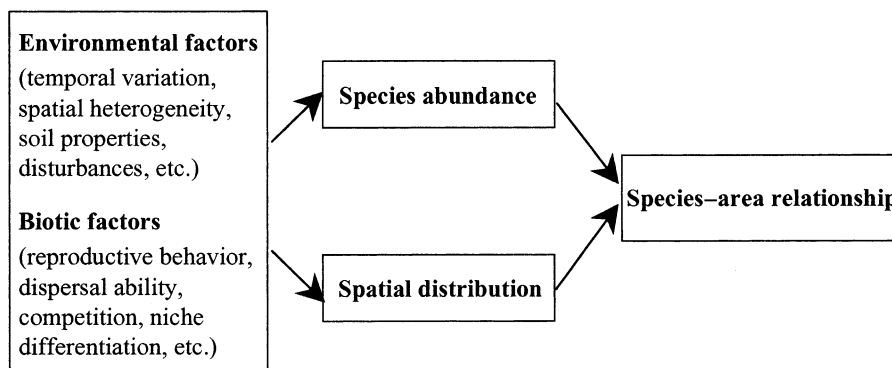


FIG. 5. A two-level conceptual model explaining the species-area relationship of a community. The species-area relationship is immediately determined by the abundances and spatial distributions of the species, while other factors are ultimate, their effects being channeled through the abundances and distributions of the species.

portant factors in interpreting species diversity. Indeed, if we go out to sample species-area data for a community, whether or not a species will be observed immediately depends on how abundant the species is and how it is distributed across space. The influences of other abiotic or biotic factors are through their effects on the abundance and spatial distribution of the species.

Interpretation of the three patterns of species diversity

We have analytically shown the general nature of the three patterns of species diversity in a community. But how well are these patterns supported by other species diversity hypotheses? Some of these hypotheses explicitly recognize the importance of abundances and spatial patterns of species in interpreting diversity (e.g., the compensatory mortality and the Janzen-Connell spacing hypotheses), whereas others do not necessarily directly rely on the patterns of abundance and spatial distributions of species but can be interpreted in that way if abundances and spatial patterns are considered (e.g., competition theory and niche hypothesis). These four diversity hypotheses are now discussed.

1. *Compensatory mortality hypothesis.*—The compensatory mortality hypothesis predicts that if more of the common species experience higher mortality, or in other words if mortality is frequency (or abundance)-dependent in a community, then a high number of species can be maintained (Connell 1978). The mechanism of frequency-dependent mortality reduces the dominance of the common species, leading to a more even species-abundance distribution, and thus allows species coexistence. The prediction of the second pattern of diversity in the present study is consistent with this hypothesis. However, it is worth noting that the reverse of this pattern may not be true, i.e., an increase in diversity is not always caused by a decrease in species dominance. This is also the case for other patterns.

2. *Janzen-Connell spacing hypothesis.*—The Janzen-Connell spacing hypothesis is the spatial version of the compensatory mortality hypothesis in tropical

tree communities. It predicts that, for common species, mortality is usually high in the neighborhood of conspecific parent trees and decreases with distance away from the parents due to the attack of distance (or density)-responsive predators (e.g., herbivores and pathogens; Janzen 1970, Connell 1971). This differential mortality process makes the spatial distribution of species more regular and reduces the probability of conspecific neighbors, thereby maintaining high species richness. Although the ubiquity of the spacing process in the tropics is controvertible (Hubbell 1979, Condit et al. 1992, Schupp 1992), the process is frequently invoked for tropical tree species (Janzen 1970, Connell 1971, Augspurger 1983, Clark and Clark 1984, Connell et al. 1984, Schupp 1992) and it provides direct support for the third pattern of diversity.

3. *Competition hypothesis.*—Although ecologists may still debate whether species compete at equilibrium or nonequilibrium conditions and how species compete for what limiting resources (Grime 1973, Newman 1973, Tilman 1982, Diamond and Case 1986), they generally agree that competition is a major force in maintaining species diversity in communities. Competition theory (e.g., the Lotka-Volterra model) predicts that species coexistence is promoted if interspecific competition is less important than intraspecific competition. Although competition coefficients that meet this requirement can occur coincidentally with a variety of relative abundance patterns, a possible consequence of intraspecific competition is that the population levels of abundant species are checked, resulting in greater species evenness in a community. This effect of competition is also recognized by other authors who wrote that “increasing intensity of [interspecific] competition should result in a decrease in species evenness and eventually species number” (Huston 1979:82). This conclusion is consistent with the second pattern of diversity found in this study. This prediction is quite reasonable because a key point in maintaining high species diversity in a community is to prevent populations of rare species from extinction (Tilman and

Pacala 1993). For that purpose, the population levels of abundant species must be reduced to release more resources that may allow the populations of rare species to sustain or grow.

Although competition theory was not formulated in the spatial context, competition primarily occurs locally, at least in plant communities, because of the sedentary nature of plants (Pacala 1986a, b). Intense local intraspecific competition tends to generate regular spatial distributions of species (Chapin et al. 1989, Abrams 1995, He and Duncan 2000), eventually resulting in species coexistence (Pacala 1986a, b). This prediction supports the third pattern of diversity, i.e., that spatial regularity of species facilitates species coexistence.

4. *Habitat niche diversification hypothesis.*—Habitat niche diversification can be envisioned either in a spatial (MacArthur 1972, Tilman 1985) or temporal context (Chesson and Huntly 1989). Here we are only interested in the former. Niche theory predicts that species richness increases if (1) the lengths of niche axes increase (i.e., more niche types are included) or (2) the width of the existing niches is narrowed (Hutchinson 1959, MacArthur 1972).

In a community, the easiest way of increasing the length of niche axes is to include more area. The effect of this condition on species richness is in agreement with the first pattern of diversity because a larger area (hence more niche types) would provide niches for more species. This condition is virtually equivalent to the habitat diversity hypothesis in explaining species–area relationships (Williams 1943).

Although increasing area is sufficient to increase niche axes, it is not the only way to do so. According to the habitat diversity hypothesis, species diversity would increase if a sample quadrat covered more niches. Condit et al. (1996) reported that diversity in long narrow rectangles is higher than in square samples. Another possible cause of this effect is that dispersal patterns of species in rectangular plots may differ from squared plots (P. Ashton, *personal comment*). In all cases, the effect of this sample shape on diversity is interesting yet understudied. More studies, both empirical and theoretical, are needed to generalize this effect.

Condition (2) may be restated to say that species richness in a community increases if the tolerance (or distribution) ranges of the species are reduced. However, two other conditions must be satisfied for this hypothesis to hold: (a) there must be sources (e.g., propagules) for incoming species in the surrounding area, and (b) the reduction must be sufficient to allow newcomers to get established. If any of these conditions fails, condition (2) will actually result in a decrease in species diversity, according to the third diversity pattern concluded from this study, because narrowing niche axes (or the distribution ranges) results in spatial aggregation of the species.

Species abundance and distribution in time

Another interesting question is: can the diversity patterns be predicted by succession theory? The answer is less clear; it all depends on how abundance and spatial patterns of the species change during succession. Although there is evidence that in some plant communities, species dominance decreases with succession (Bazzaz 1975), it can be regained in the mature stages in other communities if only the shade-tolerant species are able to establish themselves under closed canopies. This explains why no general relationship has been found between species diversity and succession (Margalef 1963, Whittaker 1965, Odum 1969).

Information is extremely scant about how spatial distributions change with succession, although findings from plant monocultures consistently show that the spatial distribution of pure stands becomes more regular with time (Ford 1975, Kenkel 1988). A similar pattern was also observed in a natural old-growth forest where the dominant early-successional Douglas-fir trees showed a clear regular distribution whereas the late-successional species presented aggregated patterns (He and Duncan 2000). In the Pasoh Forest, we compared the spatial distribution of the species between the 1987 and 1995 censuses in terms of nearest-neighbor distance, excluding from the 1995 calculation the trees that had died during this period, but including new recruits. Based on a paired *t* test involving 786 species (the species represented by a single individual had been excluded), the results showed that no significant change in mean nearest-neighbor distance had occurred between 1987 and 1995 (the mean nearest-neighbor distance was 43.8 m for 1987 and 43.5 m for 1995, $P = 0.31$). This result is not surprising given that it is based on such a short period of observation and that the forest is a homogeneously primary forest lacking major disturbances (Manokaran and LaFrankie 1990). Obviously, more field evidence, based upon long-term observations, is needed.

Diversity patterns and scales

The species–area relationship in essence is a scaling problem, i.e., how diversity sampled at one scale can be scaled up or down to other scales. The present study clearly demonstrates the importance of abundances and spatial distributions of species in determining this scaling process. However, it is worth emphasizing that the patterns investigated in this study are presumably confined to the community level. If the extent of the study area is beyond that level, some patterns may become insignificant. For instance, the negative effect of spatial aggregation on diversity (the third pattern) will probably decline or eventually cease if the extent of the study crosses beyond a defined community (P. Ashton, *personal comment*).

A significance of this study is that it resorts to multivariate patterns (i.e., species–area–abundance, spe-

cies–area–spatial distribution, in contrast to bivariate patterns such as species–area, species–abundance) for understanding community assemblage, although the way abundances and spatial distributions formulated in the study may be simplified. In addition to the models developed in this study, there is a possibility that other species–area models such as the power model may also be useful for evaluating the effects of abundances and spatial distributions on diversity. The power model is traditionally used without referring to abundances and spatial distributions of species. But this may no longer be the case as it has recently been shown that the model can arise from spatial self-similarity (Harte et al. 1999) or, on the contrary, is scale-dependent (He and Legendre 1996, Plotkin et al. 2000, Crawley and Harral 2001). Regardless of this difference, the problem now comes to be how to define the z and c values of the power model according to species abundances and spatial distribution. A recent development in spatial ecology may offer promise to this challenge. Condit et al. (2000) proposed a method to compare spatial patterns of rare and common species by controlling the confounding effects of abundance and spatial scale. Along this line, another method was subsequently developed by Ostling et al. (2000) under the assumption of self-similarity for individual species. This later method not only considers scale effect but also accounts for abundance information. The remaining question now is how to integrate this species-based approach up to the community level.

Sampling design in testing community hypotheses

The numerical analyses reported in this paper, which were based upon the species–area models developed to support the three generalizations of species diversity, lead to observations that shed light on other aspects of community ecology. The species–area curves presented in this study (Figs. 2 to 4) clearly illustrate the fact that when scientists want to distinguish among ecological situations, the field studies should use quadrats chosen to be of intermediate size (in logarithmic scale) relative to the size of the community. This recommendation is in agreement with those of Dungan et al. (*in press*) about the size of the sampling units in ecological studies. Using this quadrat size, the different mechanisms are more likely to be distinguished. The “area” value may be taken to be the minimum area that contains most species of the community of interest. Considering for instance the extent of the Pasoh Forest study area, which was 50 ha or 500 000 m² ($\ln[500\,000] = 13.12$), acceptable quadrats for such studies may range in size from (50 × 50 m), which gives a $\ln(2500) = 7.82$, to (150 × 150 m), which gives a $\ln(22\,500) = 10.02$.

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