TPB

A Spatially Explicit Neutral Model of β-Diversity in Tropical Forests

Jérôme Chave[1]

Laboratoire d'Ecologie Terrestre, CNRS UMR 5552, 13, Avenue du Colonel Roche, F-31029, Toulouse, Cedex 4, France; and Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08544-1003

and

Egbert G. Leigh Jr.

Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Republic of Panama

To represent species turnover in tropical rain forest, we use a neutral model where a tree's fate is not affected by what species it belongs to, seeds disperse a limited distance from their parents, and speciation is in equilibrium with random extinction. We calculate the similarity function, the probability $F(r)$ that two trees separated by a distance r belong to the same species, assuming that the dispersal kernel $P(r)$, the distribution of seeds about their parents and the prospects of mortality and reproduction, are the same for all trees regardless of their species. If $P(r)$ is radially symmetric Gaussian with mean-square dispersal distance σ, $F(r)$ can be expressed in closed form. If $P(r)$ is a radially symmetric Cauchy distribution, then, in two-dimensional space, $F(r)$ is proportional to $1/r$ for large r. Analytical results are compared with individual-based simulations, and the relevance to field observations is discussed. © 2002 Elsevier Science (USA)

Key Words: data diversity; long-distance dispersal; neutral model; tropical forest

1. INTRODUCTION

During the last 20 years, our understanding of the processes maintaining tree diversity at a given tropical site has greatly increased, thanks to the establishment of large permanent sampling plots where all stems > 1 cm dbh (diameter at breast height, which is stem diameter 1.3 m above the ground) are mapped, marked, measured and identified (Condit, 1995). The first of these large plots was the 50-ha plot on Barro Colorado Island (BCI), Panama, first censused in 1982 (Hubbell and Foster, 1983, 1986; Condit, 1995; Leigh, 1999). BCI's 50-ha plot is now just one of more than 15 large sample plots in the Neotropics, Africa and South-East

Asia that have been censused and monitored according to a protocol established by the Smithsonian Tropical Research Institute's Center for Tropical Forest Science (Manokaran *et al.*, 1990; Condit, 1998).

We know much less about the factors which govern β-diversity (species turnover) as manifested in the divergence of tree species composition between forest plots in different places, and how differences in soil or climate affect this divergence. Indeed, the facts of species turnover among tropical trees are only just now being elucidated, through the study of regional networks of small forest plots. Ashton (1964, 1976) and Ashton and Hall (1992), the pioneers in this question, established a series of small plots in South-East Asia. Other regional systems of plots of 1 or 2 ha apiece have since been established in Amazonian Peru (Terborgh and Andresen, 1998; Pitman *et al.*, 2001), Ecuador (Pitman *et al.*, 1999) and central Panama (Pyke *et al.*, 2001). Very little

has yet been done to order these new facts on β-diversity (Pitman *et al.*, 2001; Condit *et al.*, 2002). Using an extension of Hubbell's (2001) neutral theory of tree diversity, this paper will show how speciation and limited seed dispersal can contribute to species turnover.

One function of BCI's 50-ha plot was to test theories of why tropical forests have so many tree species. Prominent among these was Hubbell's (1979) neutral theory, which embodied the fundamental insight (Mac Arthur and Wilson, 1967) that diversity represents a balance between speciation and extinction. Hubbell (1979) supposed that extinction is a purely random process. All trees have the same prospects of mortality and recruitment, regardless of their species, and each dead tree is immediately replaced by the young of a tree chosen at random from among its survivors in the forest. The independent accidents of which trees reproduce, and which die first, change the abundances of different tree species, and drive some to extinction.

How can such a null model be useful? Hubbell's (1979) assumption that a plant's fate is independent of what species it or its neighbors belong to is false for seeds and seedlings. As Janzen (1970) and Connell (1971) predicted, seeds and seedlings with many conspecific neighbors or close to their parent plants are more likely to die (Givnish, 1999; Wills and Condit, 1999; Wright, 2002; Harms *et al.*, 2000), probably because of the disproportionate influence of specialized pests and of pathogens spreading from conspecific neighbors. Although seeds fall close to their parents (Hubbell *et al.*, 1999), in most tropical tree species, the proportion of saplings belonging to a given tree's species does not increase when one approaches the tree (Condit *et al.*, 1992; Okuda *et al.*, 1997). Moreover, the rate of appearance onto 10×10 or 20×20 m subplots of saplings of a given species over 1 cm dbh per adult of the same species is lower on subplots with higher basal area (total cross-sectional area of the trunks) of adult conspecifics (Wills *et al.*, 1997, Wills and Condit, 1999).

On the other hand, these effects are much weaker for large trees ($\geqslant 10$ cm dbh) at larger scales. For most species, the rate of appearance of saplings per adult on subplots 50 m or more on a side does not depend detectably on the density or basal area of adults conspecifics on the subplot (Wills *et al.*, 1997). Moreover, plot-scale analyses of the dynamics of individual tree species reveals density-dependent population regulation in only very few species (Hubbell *et al.*, 1990). This suggests that density dependence may not affect the dynamics of large trees. Although Hubbell's model fails

for small saplings on local scales, can it work for larger trees on larger scales?

Another problem with Hubbell's (1979) model is that it assumes a panmictic community totally isolated from the rest of the forest, leaving no room for metapopulation processes. In a newer version of his model, when a tree $\geqslant 10$ cm dbh dies, its replacement has probability $1 - m$ of being chosen at random at that plot, and probability m of being chosen from a large, panmictic pool of N source trees (Hubbell, 1997). In the source pool, each new individual has probability v of being a new species. This speciation balances extinction, so the pool's distribution of tree species abundance follows a log series characterized by the parameter $\alpha = Nv$ (Watterson, 1974). This makeshift enabled Hubbell (1997) to fit the distribution over species of trees $\geqslant 10$ cm dbh on plots of 50 ha or less by adjusting the parameters m and α.

Hubbell's (1997) model faces two challenges. First, its picture of speciation is too simplistic (Hubbell, 2001): species rarely begin as single mutant individuals. Nonetheless, most species may well evolve from peripheral isolates of ancestral species (Mayr, 1954). According to Hubbell (2001), the results of his model will be little altered if species begin from small isolated populations rather than single individuals. Second, Hubbell's (1997) model cannot predict species turnover, because a local community's species composition depends only on its relation to the source pool, not on the species present in neighboring communities. Terborgh *et al.* (1996) and Pitman *et al.* (1999) argued that widely separated plots in western Amazonia were more similar in species composition than seemed plausible under Hubbell's neutral model. To evaluate their objection, we need a version of the neutral model for a very large forest where seeds disperse only a limited distance from their parents, as is the case for any tree (Hubbell *et al.*, 1999; Harms *et al.*, 2000). Tree species turnover has traditionally been ascribed to habitat differences, not to dispersal limitation (Whittaker, 1972), often on good evidence (Ashton, 1964, 1976; Gentry, 1982, 1988). Can a null model that incorporates the joint effects of speciation and limited seed dispersal account for how the divergence in tree species composition between two plots increases with distance between the plots, or must we invariably invoke the effects of environmental heterogeneity?

One measure of species turnover, or β-diversity (change in species composition of two plots with distance between them) is how rapidly increasing r decreases the probability $F(r)$ that two randomly chosen trees a distance r apart are the same species (Condit *et al.*, 2002). Leigh *et al.* (in press), have calculated $F(r)$,

using a population genetics model of Nagylaki (1974) to represent a suitably modified version of Hubbell's model where seeds are dispersed about each parent, regardless of species, according to the same radially symmetric Gaussian density. Theoreticians have extended this type of model to various other dispersal kernels (Durrett and Levin, 1996; Hubbell, 2001; Chave *et al.*, 2002). In this paper, we provide a general and exact derivation for $F(r)$ using any radially symmetric dispersal kernel, and apply it to the Gaussian and Cauchy dispersal kernels.

Population geneticists such as Malécot (1948), Weiss and Kimura (1965), Maruyama (1972), Nagylaki (1974, 1976), and Sawyer (1976, 1977a,b) devised very similar models to solve a problem posed by Wright (1943) and Kimura (1953): given a multi-allelic genetic locus in a continuously distributed population where offspring disperse only a limited distance from their parents, or a population on an archipelago where only nearby islands exchange migrants, what is the correlation between allelic states at this locus in individuals separated by a distance r? Such models have been used as null hypotheses to probe causes of spatial patterns in the genetic composition of selected populations, including humans (Kimura and Ohta, 1971; Cavalli-Sforza *et al.*, 1994; Rousset, 2000). Nagylaki's (1974) model readily translates into Hubbell's null model of tree diversity if we let an individual in a continuously distributed population represent a tree in a continuously distributed, multi-species forest and a haploid individual's allele at the multi-allelic locus in question represent a tree's species. Harada *et al.* (1997) used this model to calculate how, in a continuous monospecific stand where plants reproduced both clonally and sexually, the probability that two plants were of different genotype increases with distance between them. Here, clones propagate only a limited distance but sexually produced seeds are dispersed uniformly through the population.

To develop our model's predictions, we first derive $F(r)$ when seeds are dispersed about each parent in a radially symmetric Gaussian distribution. This formula is known (Malécot, 1948) and approximations for it (Nagylaki, 1976) and asymptotic results (Sawyer, 1977a) have been obtained, but we believe a detailed derivation would benefit readers. Indeed, current derivations are abbreviated, hard to find, or intended for mathematicians, and colonies are often substituted for individuals. Next, we let the seed dispersal kernel be proportional to $1/r^3$ when r is large, which implies that mean-square dispersal distance is infinite, thus violating the assumptions of Sawyer's (1977a) limit theorem. This leads us to new results. Next, we use numerical simulations of our model to test the accuracy of our model's predictions of the average value of $F(r)$, for given r at equilibrium, assess the variability of $F(r)$ about this average, and learn how initial conditions affect the approach to equilibrium. Finally, we discuss how to test the model with data from sample plots of forest.

2. THE MODEL

Consider two plots A and B, with known floristics, with S species in all. Let the proportion of individuals belonging to species s be p_s^A on plot A and p_s^B on plot B, where p_s^A and p_s^B can be 0. The similarity of species compositions of these two plots may be measured by the index of codominance (Leigh *et al.*, 1993), the chance that two trees chosen at random, one from plot A and the other from plot B, are the same species, or

$$F(A,B) = \sum_{s=1}^{S} p_s^A p_s^B.$$

In population genetics, this index is the coefficient of consanguinity between samples from two parts of a population, that is the chance that genes from the same locus, one from sample A and the other from sample B, are the same allele (Crow and Kimura, 1970). In ecology $1 - F(A,A)$ measures local, or α-diversity, and is related to Simpson's index (Simpson, 1949; Magurran, 1988). Similarity, indices $\mathscr{S}(A,B)$ normalize $F(A,B)$ to make $\mathscr{S}(A,A) = \mathscr{S}(B,B) = 1$. Thus, the Morisita–Horn similarity index $\mathrm{MH}(A,B)$ is $2F(A,B)/[F(A,A)+F(B,B)]$ (Horn, 1966) while Nei (1987) calls $I(A,B) = F(A,B)/\sqrt{F(A,A)F(B,B)}$ the genetic identity. We focus on $F(A,B)$ because, unlike normalized indices, codominance between two widely separated forest plots A and B is an unbiased estimator of the probability that a randomly chosen tree near A and a randomly chosen tree near B are the same species (Leigh *et al.*, 1993).

Assuming that $F(A,B)$ depends only on the distance between plots A and B, and not on different environmental conditions in these plots, we seek the probability $F(r)$ that two trees a distance r apart are the same species, given that seeds disperse a limited distance from their parents. Our problem has analogs in spaces of one or three dimensions, which we also consider. We accordingly let $F_d(r)$ represent the probability that two organisms separated by a Euclidean distance r in d-dimensional space are the same species. We assume that trees are distributed homogeneously over a surface, with a density of ρ per unit area.

We begin by letting $F_2(\mathbf{x}, \mathbf{y}, t)$ be the probability that a tree chosen randomly at time t from a neighborhood $dS_\mathbf{x} = dx_1\, dx_2$ including the site $\mathbf{x} = \{x_1, x_2\}$ is conspecific with a tree simultaneously chosen in a neighborhood $dS_\mathbf{y}$ including the site $\mathbf{y} = \{y_1, y_2\}$. How is $F(\mathbf{x}, \mathbf{y}, t + dt)$ related to $F(\mathbf{x}, \mathbf{y}, t)$? To find out, we assume that (i) the spatial distribution of trees is a continuous Poisson point process whose mean is ρ; (ii) any tree alive at time t has probability dt of dying by time $t + dt$ independent of the fate of any other tree, so that the average lifetime of any tree is one time unit, regardless of its species; (iii) a proportion $P(\mathbf{x}, \mathbf{y})\, dS_\mathbf{y}$ of the seeds of a tree at site $\mathbf{x}$ land in the neighborhood $dS_\mathbf{y}$ surrounding $\mathbf{y}$, where $P(\mathbf{x}, \mathbf{y})$ is the "dispersal kernel" of each tree's seeds; and (iv) each new tree has probability v of being an entirely new species.

To calculate $F_2(\mathbf{x}, \mathbf{y}, t + dt)$ from $F_2(\mathbf{x}, \mathbf{y}, t)$, recall that with probability $2dt$, one of the two trees dies between time t and $t + dt$. Let the dying tree be the one at $\mathbf{x}$, and let it be replaced immediately by the young of a nearby tree. Call the probability that this parent is conspecific with the tree at $\mathbf{y}$, $Q(\mathbf{x}, \mathbf{y}, t)$. If the young has a probability v of being an entirely new species, then

$$F_2(\mathbf{x}, \mathbf{y}, t + dt) = (1 - 2dt)F_2(\mathbf{x}, \mathbf{y}, t) + (2dt)(1 - v)Q(\mathbf{x}, \mathbf{y}, t). \quad (2.1)$$

The continuous time limit of this equation is

$$\frac{\partial F_2(\mathbf{x}, \mathbf{y}, t)}{\partial t} = -2F_2(\mathbf{x}, \mathbf{y}, t) + 2(1 - v)Q(\mathbf{x}, \mathbf{y}, t). \quad (2.2)$$

To find $Q(\mathbf{x}, \mathbf{y}, t)$, recall that the probability that the tree at $\mathbf{x}$ is replaced by the young of a tree in the neighborhood $dS_\mathbf{u}$ of $\mathbf{u} = \{u_1, u_2\}$ is $P(\mathbf{u}, \mathbf{x})\, dS_\mathbf{u}$, in which case this young has probability $(1 - v)F_2(\mathbf{u}, \mathbf{y}, t)$ of being conspecific with the tree at y. If the tree at $\mathbf{x}$ is replaced by a young of a tree in a neighborhood $dS_\mathbf{y}$ of the tree at $\mathbf{y}$, its parent has probability $1/(\rho\, dS_\mathbf{y})$ of being the tree at $\mathbf{y}$, and probability $1 - 1/(\rho\, dS_\mathbf{y})$ of being another tree in the neighborhood, which latter would have probability $F_2(\mathbf{y}, \mathbf{y}, t)$ of being conspecific with the tree at $\mathbf{y}$. Notice that $1 - 1/(\rho\, dS_\mathbf{y})$ is positive only if $dS_\mathbf{y} > 1/\rho$, that is if there is at least one individual in the neighborhood $dS_\mathbf{y}$. This condition sets the lattice spacing in the fine-grained model. $Q(\mathbf{x}, \mathbf{y}, t)$ may be expressed as

$$\int_\mathbf{u} F_2(\mathbf{u}, \mathbf{y}, t)P(\mathbf{u}, \mathbf{x})\, dS_\mathbf{u} + \frac{1 - F_2(\mathbf{y}, \mathbf{y}, t)}{\rho\, dS_\mathbf{y}} P(\mathbf{y}, \mathbf{x})\, dS_\mathbf{y}$$

$$= \int_\mathbf{u} F_2(\mathbf{u}, \mathbf{y}, t)P(\mathbf{u}, \mathbf{x})\, dS_\mathbf{u}$$

$$+ \frac{1 - F_2(\mathbf{y}, \mathbf{y}, t)}{\rho} P(\mathbf{y}, \mathbf{x}). \quad (2.3)$$

Notice that in these equations the condition $dS_\mathbf{u} > 1/\rho$ can be relaxed without leading to impossible results (i.e., negative probabilities).

Now suppose that the probability two trees are the same species depends only on their *relative* positions, so that $F_2(\mathbf{x}, \mathbf{y}, t) = F_2(\mathbf{x} - \mathbf{y}, t)$ and let $P(\mathbf{x}, \mathbf{y}) = P(\mathbf{x} - \mathbf{y})$. Then the master equation is

$$\frac{\partial F_2(\mathbf{x}, t)}{\partial t} = -2F_2(\mathbf{x}, t) + 2(1 - v)$$

$$\times \left(\int_\mathbf{u} P(\mathbf{u})F_2(\mathbf{x} - \mathbf{u}, t)\, dS_\mathbf{u} + \frac{1 - F_2(\mathbf{0}, t)}{\rho} P(\mathbf{x}) \right). \quad (2.4)$$

At equilibrium

$$F_2(x_1, x_2)$$

$$= (1 - v)\left(\int_{u_1, u_2} P(u_1, u_2)F_2(x_1 - u_1, x_2 - u_2)\, du_1\, du_2 + \frac{1 - F_2(0, 0)}{\rho} P(x_1, x_2) \right). \quad (2.5)$$

Malécot (1948, Eq. (1), p. 57; 1969, Eq. (3.3.1), p. 68) first derived an equation like (2.5) for the correlation in allelic state of genes at the same diallelic locus sampled from two individuals at a distance r apart in a diploid population (so that he replaces our ρ by 2δ) where successive generations are distinct (so that he replaces our v by $1 - (1 - k)^2 \simeq 2k$).

3. MALÉCOT'S INTEGRAL EQUATION

Now we derive a formal solution of Eq. (2.5) similar to that of Malécot (1948). First, we take the Fourier transform of Eq. (2.5). Let $p(k, m)$ be the Fourier transform of $P(x, y)$ and $f_2(k, m)$ that of $F_2(x, y)$. Then

$$f_2(k, m) = (1 - v)$$

$$\times \left(f_2(k, m)\, p(k, m) + \frac{1 - F_2(0, 0)}{\rho} p(k, m) \right). \quad (3.1)$$

Since $|(1 - v)p(k, m)| < 1$, we may set

$$f_2(k, m) = \frac{1 - F_2(0, 0)}{\rho} \frac{(1 - v)p(k, m)}{1 - (1 - v)p(k, m)}$$

$$= \frac{1 - F_2(0)}{\rho} \sum_{j=1}^{\infty} (1 - v)^j p(k, m)^j. \quad (3.2)$$

Assume next that $P(x, y)$ and $F_2(x, y)$ are functions only of $r = \sqrt{x^2 + y^2}$. Then their Fourier transforms p and

f_2 are functions only of $q = \sqrt{k^2 + m^2}$, and Eq. (3.2) becomes

$$f_2(q) = \frac{1 - F_2(0)}{\rho} \sum_{j=1}^{\infty} (1 - v)^j p(q)^j. \qquad (3.3)$$

The two-dimensional Fourier transform of an isotropic function $Z(r)$ and its inverse are

$$z(q) = 2\pi \int_{r=0}^{\infty} Z(r) J_0(rq) r \, dr,$$

$$Z(r) = \frac{1}{2\pi} \int_{q=0}^{\infty} z(q) J_0(rq) q \, dq, \qquad (3.4)$$

where $J_0(x)$ is the Bessel function of the first kind and order 0. Taking the inverse Fourier transform of (3.3), we find

$$F_2(r) = \frac{1 - F_2(0)}{\rho} \frac{1}{2\pi} \int_{q=0}^{\infty} \sum_{j=1}^{\infty} (1 - v)^j p(q)^j J_0(rq) q \, dq. \qquad (3.5)$$

Here again, the series is absolutely convergent for all $v > 0$. Therefore, we can use Fubini's theorem to interchange the sum and integral as follows:

$$F_2(r) = \frac{1 - F_2(0)}{\rho} \frac{1}{2\pi} \sum_{j=1}^{\infty} (1 - v)^j \int_{q=0}^{\infty} p(q)^j J_0(rq) q \, dq. \qquad (3.6)$$

So far, we have assumed nothing about the dispersal kernel $P(r)$ except that it is a probability density (which implies that it has a Fourier transform).

Equation (3.6) has a much simpler form if the dispersal kernel $P(r)$ has a finite variance $2\sigma^2$, and if $r \gg \sigma$. To be more specific, let us define σ^2 by

$$\sigma^2 = \int_{x,y} x^2 P(x, y) \, dx \, dy = \int_{x,y} y^2 P(x, y) \, dx \, dy. \qquad (3.7)$$

When $r \gg \sigma$ we may neglect the term multiplying $1 - F_2(0, 0)$ in Eq. (2.5) and obtain

$$F_2(x, y) = (1 - v) \int P(w, z) F_2(x - w, y - z) \, dw \, dz. \qquad (3.8)$$

If the dispersal kernel $P(r)$ decreases with r faster than a negative exponential (as is true for a Gaussian dispersal kernel) we may expand $F_2(x - w, y - z)$ in Taylor series around x, y and neglect terms higher than second order.

We, thereby, obtain

$$F_2(x - w, y - z) = F_2(x, y) - \left(w \frac{\partial F_2(x, y)}{\partial x} + z \frac{\partial F_2(x, y)}{\partial y} \right)$$
$$+ \frac{1}{2} \left(w^2 \frac{\partial^2 F_2(x, y)}{\partial x^2} + 2wz \frac{\partial^2 F_2(x, y)}{\partial x \partial y} \right.$$
$$\left. + z^2 \frac{\partial^2 F_2(x, y)}{\partial y^2} \right). \qquad (3.9)$$

Since $P(x, y)$ is isotropic, $\int_{x,y} xy P(x, y) \, dx \, dy = 0$. Substituting Eq. (3.9) into Eq. (3.8), we obtain

$$F_2(x, y) = \frac{(1 - v)\sigma^2}{2v} \left(\frac{\partial^2 F_2(x, y)}{\partial x^2} + \frac{\partial^2 F_2(x, y)}{\partial y^2} \right)$$
$$= \frac{(1 - v)\sigma^2}{2v} \Delta F_2(x, y), \qquad (3.10)$$

where Δ is the Laplacian operator.

If we rewrite Eq. (3.10) in polar coordinates, and assume $v \ll 1$, we obtain the Bessel equation

$$\frac{d^2 F_2(r)}{dr^2} + \frac{1}{r} \frac{dF_2(r)}{dr} = (2v/\sigma^2) F_2. \qquad (3.11)$$

The only positive solution such that $\lim_{r \to \infty} F_2(r) = 0$ is

$$F_2(r) = c K_0 \left(\frac{r\sqrt{2v}}{\sigma} \right). \qquad (3.12)$$

$K_0(x)$ is the modified Bessel function of zeroth order and the second kind, and c is a constant. As we shall show almost immediately (Eq. (4.7)), Eq. (3.12) is accurate for $r \gg \sigma$, showing that no harm came from ignoring terms in the Taylor expansion higher than second order. On the other hand, $K_0(r)$ diverges logarithmically as r approaches 0: Eq. (3.12) cannot be valid for small r. For large r, the function $K_0(r)$ is further approximated by

$$K_0(r) \simeq \sqrt{\frac{\pi}{2r}} \exp(-r)$$

which is the form suggested in Harada *et al.* (1997) for the same model, but in a different biological context.

4. GAUSSIAN DISPERSAL KERNELS

In this section, we solve Eq. (3.6) when the dispersal kernel is a radially symmetric Gaussian density, show how large r must be for $F_2(r)$ to approach the solution of Eq. (3.12), and evaluate the coefficient c in that equation.

4.1. Two Dimensions

If the Fourier transform or characteristic function (Feller, 1971) of the probability density $P(r)$ is $p(q)$, $p(q)^j$ is the Fourier transform of the probability density of a sum of j independent random variables, each with probability density $P(r)$. The Fourier transform of the radially symmetric Gaussian density $P(r) = (1/2\pi\sigma^2)\exp(-(r^2/2\sigma^2))$, is $p(q) = \exp(-\sigma^2 q^2/2)$. Therefore, the probability density whose Fourier transform is $\exp(-j\sigma^2 q^2/2)$ must be $(1/2\pi j\sigma^2)\exp[-r^2/(2j\sigma^2)]$.

If we use the above expressions in Eq. (3.6), then

$$F_2(r) = \frac{1}{2\pi\sigma^2}\frac{1 - F_2(0)}{\rho}$$
$$\times \sum_{j=1}^{\infty}\frac{(1-v)^j}{j}\exp\left(-\frac{r^2}{2j\sigma^2}\right). \qquad (4.1)$$

Equation (4.1) corresponds to Malécot's (1948, p. 62) solution for a Gaussian dispersal kernel, his $2k - k^2$ corresponds to our v, and his 2δ to our ρ. To find $F_2(0)$, we set $r = 0$ in Eq. (4.1) to obtain

$$F_2(0) = \frac{1}{2\pi\sigma^2}\frac{1 - F_2(0)}{\rho}\sum_{j=1}^{\infty}\frac{(1-v)^j}{j}. \qquad (4.2)$$

Since $\ln(1/v) = \sum_{j=1}^{\infty}(1-v)^j/j$, we find

$$F_2(0) = \frac{\ln(1/v)}{2\rho\pi\sigma^2 + \ln(1/v)}. \qquad (4.3)$$

Community ecologists know $1 - F_2(0)$ as Simpson's diversity index. For monodominant communities, $1 - F_2(0)$ is nearly 0. Substituting Eq. (4.3) into Eq. (4.1), we find

$$F_2(r) = \frac{1}{2\rho\pi\sigma^2 + \ln(1/v)}\sum_{j=1}^{\infty}\frac{(1-v)^j}{j}\exp\left(-\frac{r^2}{2j\sigma^2}\right). \qquad (4.4)$$

When does this solution approach the approximations of Nagylaki (1974) and Sawyer (1977a)? If we set $C = 1/[2\pi\sigma^2 + \ln(1/v)]$, then Nagylaki's approximation for Eq. (4.4) is (Leigh *et al.*, in press)

$$F_2^{Nagylaki}(r) = 2C\left(K_0\left(\frac{r\sqrt{2v}}{\sigma}\right) - K_0\left(\frac{r\sqrt{2}}{\sigma}\right)\right), \qquad (4.5)$$

where his $2v$ corresponds to our v (we assume overlapping, he assumes distinct, generations) and his 2ρ to our ρ (we consider haploid, he, diploids).

In Eq. (4.4), let $v < 10^{-6}$, so that we can replace $(1 - v)^j$ by $\exp(-jv)$, and let $r \gg \sigma$. The sum in Eq. (4.4) is a Riemann series

$$\sum_{j=1}^{\infty}\frac{(1-v)^j}{j}\exp\left(-\frac{r^2}{2j\sigma^2}\right)$$
$$\simeq \int_{y=0}^{\infty}\exp\left(-vy - \frac{r^2}{2y\sigma^2}\right)\frac{dy}{y}. \qquad (4.6)$$

This integral is $2K_0(r\sqrt{2v}/\sigma)$ (Gradshteyn and Ryzhik, 2000, (3.471.9)). Therefore,

$$F_2(r) \simeq \frac{1}{2\rho\pi\sigma^2 + \ln(1/v)}2K_0\left(\frac{r\sqrt{2v}}{\sigma}\right). \qquad (4.7)$$

This approximation is equivalent to that of (3.12), only we now know the coefficient c of (3.12) is equal to $2C$. If we now remember that when $r \gg \sigma$, $K_0(r\sqrt{2v}/\sigma) \gg K_0(r\sqrt{2}/\sigma)$, this result agrees with Eq. (4.5). Numerical evaluation of (4.4) shows that Eq. (4.7) is accurate to within 1% for $r \geqslant 1.149\sigma$ if $v = 10^{-6}$.

Sawyer (1977a, Eq. (3.2)) proved that Eq. (3.12) is valid for $r \gg \sigma$ for any dispersal kernel with finite variance, if we set

$$c = \frac{2}{2\rho\pi\sigma^2 + \ln(1/v) + C_0}$$

with C_0 a constant that depends only on the shape of the dispersal kernel $P(r)$.

Now let $r \ll \sigma$ and set $\exp(-r^2/2j\sigma^2) \simeq 1 - r^2/2j\sigma^2$ in (4.4) to obtain

$$F_2(r) \simeq \frac{1}{2\rho\pi\sigma^2 + \ln(1/v)}\sum_{j=1}^{\infty}\frac{(1-v)^j}{j}\left(1 - \frac{r^2}{2j\sigma^2}\right)$$
$$= F_2(0) - \frac{1}{2\rho\pi\sigma^2 + \ln(1/v)}\frac{r^2\pi^2}{12\sigma^2}. \qquad (4.8)$$

Here we have used the fact that when $v < 0.01$, $\sum_{j=1}^{\infty}(1-v)^j/j^2 \simeq \pi^2/6$. Nagylaki's (1974) equation agrees rather poorly with (4.8) for small positive r. Numerical evaluation of (4.4) shows that Eq. (4.8) is accurate to within 1% for $r \leqslant 0.827\sigma$ if $v = 10^{-3}$, and for $r \leqslant 1.00\sigma$ if $v = 10^{-6}$.

4.2. Multi-Dimensional Gaussian Dispersal Kernels

We may generalize Eq. (4.4) to Euclidean spaces of any dimension d. The radially symmetric Gaussian dispersal kernel is

$$P(x_1, \ldots, x_d) = \frac{1}{(\sqrt{2\pi}\sigma)^d}\exp\left(-\frac{\sum_{i=1}^{d}x_i^2}{2\sigma^2}\right). \qquad (4.9)$$

Since the Fourier transform $p(q)$ of the radially symmetric Gaussian density $P(r)$ is $\exp(-\sigma^2 q^2)$ for any

dimension d we find, as in Eq. (4.1)

$$F_d(r) = \frac{1 - F_d(0)}{\rho} \sum_{j=1}^{\infty} \frac{(1-v)^j}{(\sigma\sqrt{2j\pi})^d} \exp\left(-\frac{r^2}{2j\sigma^2}\right). \quad (4.10)$$

As in the two-dimensional case, we set $(1-v)^j = \exp(-vj)$, replace the sum by an integral and use formula (3.471.9) in Gradshteyn and Ryzhik (2000) to obtain for $r > \sigma$

$$F_d(r) = \frac{1 - F_d(0)}{\rho} \frac{2}{(2\pi\sigma^2)^{d/2}} \left(\frac{r^2}{2v\sigma^2}\right)^{2-d/4}$$
$$\times K_{d/2-1}\left(\frac{r\sqrt{2v}}{\sigma}\right). \quad (4.11)$$

For biological problems, only the versions of this formula in one, two, or three dimensions are useful. Equation (4.11) is particularly simple for $d = 1$ or 3, because $K_{1/2}(x) = K_{-1/2}(x) = \sqrt{(\pi/2x)}\exp(-x)$. When $d = 1$

$$F_1(r) = \frac{1}{1 + \rho\sigma\sqrt{2v}} \exp\left(-\frac{r\sqrt{2v}}{\sigma}\right). \quad (4.12)$$

$F_1(r)$ declines exponentially with distance (Malécot, 1948; Kimura and Weiss, 1964; Nagylaki, 1974). Unlike the two-dimensional case, approximation (4.12) for $F_1(r)$ does not diverge as r approaches 0. Indeed, numerical evaluation shows that if $v \ll 1$, the value of $F_1(0)$ estimated from Eq. (4.12) approximates the exact solution quite closely.

In three dimensions, we find

$$F_3(r) = \frac{1 - F_3(0)}{2\pi\rho\sigma^2 r} \exp\left(-\frac{r\sqrt{2v}}{\sigma}\right). \quad (4.13)$$

We must compute $F_3(0)$ from (4.10), because (4.13) has no clear limit as r approaches 0. With an error not exceeding 1% for $v \leqslant 10^{-4}$, we may set

$$\sum_{j=1}^{\infty} \frac{(1-v)^j}{j^{3/2}} \simeq \sum_{j=1}^{\infty} \frac{1}{j^{3/2}} = \zeta(3/2) \simeq 2.612,$$

where $\zeta(s) = \sum_{j=1}^{\infty} 1/j^s$ is Riemann's zeta function. Then

$$F_3(r) = \frac{\sqrt{2\pi}}{\rho(2\pi\sigma^2)^{3/2} + \zeta(\tfrac{3}{2})r} \frac{\sigma}{r} \exp\left(-\frac{r\sqrt{2v}}{\sigma}\right). \quad (4.14)$$

As dimensionality d increases from 1 to 3, $F_d(0)$ becomes progressively less sensitive to the speciation rate v. $F_1(0) = 1/[1 + \rho\sigma\sqrt{2v}]$ depends on $\sqrt{v}$, $F_2(0) = 1/[1 + 2\pi\rho\sigma^2/\ln(1/v)]$ depends only logarithmically on v, and $F_d(0)$, $d \geqslant 3$ does not depend on v at all, provided v is small enough. Moreover, as the speciation rate v approaches 0, $F_d(r) \sim 1/r^{d-2}$ for large r, as it should,
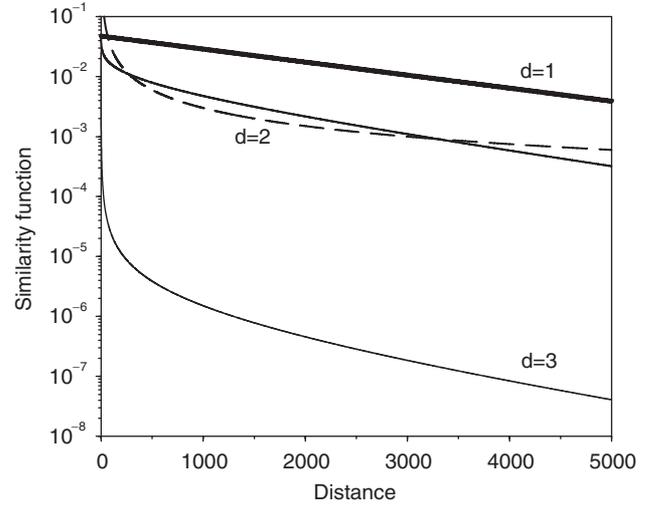

FIG. 1. Theoretical predictions for the similarity function in one, two, and three dimensions of space with the Gaussian dispersal kernel (full lines) and with the Cauchy dispersal kernel (dashed line) in two dimensions of space. For the Gaussian dispersal kernel, $\sigma = 8$ and $v = 10^{-6}$ in all three cases, and for the Cauchy kernel, $c = 1$. For a better comparison, the function corresponding to the Cauchy kernel has been multiplied with 3.

according to a powerful theorem of Bramson and Griffeath (1980). The formula for $F_3(0)$ shows that in the three-dimensional case with limited dispersal, speciation is not needed to maintain diversity. The similarity in one, two and three dimensions of space are compared in Fig. 1.

A limit theorem of Sawyer (1977a) completes this picture. It establishes that, for dispersal kernels with finite moments:

(1) In one dimension, for any dispersal kernel such that $\int r^5 P(r)\,dr < \infty$, $F_1(r)$ is proportional to Eq. (4.12), with a correction term of magnitude $O(v(1+1/r))$.

(2) In two dimensions, for any dispersal kernel such that $\int r^3 P(r)\,dr^2 < \infty$, $F_2(r)$ is proportional to Eq. (4.7) to leading order, with a correction term of magnitude $O(v)$.

(3) In three dimensions, for any dispersal kernel such that $\int r^2 P(r)\,dr^3 < \infty$, $F_3(r)$ is proportional to Eq. (4.13) to leading order, with a correction term of magnitude $O(v^{1/2})$.

Here, we say that a function $f(r)$ is proportional to a function $g(r)$ iff $\lim_{r\to\infty}(f(r)/g(r))$ is a constant independent of r. Therefore, for any dispersal kernel $P(r)$ that decreases fast enough for large r, Eqs. (4.12), (4.7), and (4.14), accurately describe the behavior of $F_d(r)$, $d \leqslant 3$ for large r. For slightly weaker hypotheses of this limit theorem, see Sawyer (1977a).

5. POWER-LAW DISPERSAL KERNELS

If the third moment of the dispersal kernel is not finite, Sawyer's limit theorem does not apply. Dispersal kernels with infinite variance were long considered irrelevant for ecological problems, because finite samples have finite variances (for a recent discussion, see Clark *et al.*, 2001). In some studies, however, the next item sampled might greatly increase the whole sample's variance, no matter how many were sampled before, in which case the sample may be best fit by a distribution with infinite variance. Biologists have long realized that exponentially bounded dispersal kernels cannot account for the speed with which trees reoccupied regions vacated by retreating glaciers at the end of the Pleistocene as measured by the pollen record (Skellam, 1951; Davis, 1963; Clark *et al.*, 1998). Clark (1998), using the formalism developed by Kot *et al.* (1996), showed that "fat-tailed" dispersal kernels, where some seeds disperse quite long distances, can explain the speed with which trees spread in the Pleistocene. One suggested dispersal kernel is (Clark *et al.*, 1999)

$$P(r) = \frac{p}{\pi c^2 (1 + r^2/c^2)^{p+1}}. \tag{5.1}$$

For computational convenience, we have replaced the u in Clark *et al.* (1999), by c^2. The kth moment is finite if and only if $k < 2p$. Thus, Sawyer's theorem is valid if and only if $p > \frac{3}{2}$. Clark *et al.* (1999) fitted dispersal kernels of three types, including (5.1) and the radially symmetric Gaussian, to the distributions of dispersal distances < 100 m of seeds of 24 tree species using a maximum likelihood method. In 14 of these 24 tree species, seed dispersal was best described by dispersal kernel (5.1). For 11 of the 14 species, the value of p which best fit the data was < 1; for nine, it was $< \frac{1}{2}$, the smallest value tried.

What form does $F(r)$ take when the dispersal kernel is the "fat-tailed" (5.1)? In two dimensions, the Fourier transform of (5.1) is (Gradshteyn and Ryzhik, 2000, formula (6.565.4))

$$p(q) = 2\pi \int_0^\infty \frac{pc^{2p}}{\pi(c^2 + r^2)^{p+1}} J_0(rq) r \, dr$$

$$= 2p \left(\frac{cq}{2}\right)^p \frac{K_p(cq)}{\Gamma(p+1)}, \tag{5.2}$$

where, as above, K_p is the modified Bessel function of the second kind. Here, the median dispersal distance is

$c\sqrt{3}$, and $F_2(r)$ is

$$F_2(r) = \frac{1 - F_2(0)}{\rho} \frac{1}{2\pi} \sum_{j=1}^\infty (1 - v)^j$$

$$\times \int_{q=0}^\infty \left(2p\left(\frac{cq}{2}\right)^p \frac{K_p(cq)}{\Gamma(p+1)}\right)^j J_0(rq) q \, dq.$$

When $p = \frac{1}{2}$, Eq. (5.1) is the two-dimensional Cauchy density $c/[2\pi(c^2 + r^2)^{3/2}]$. This density, like the corresponding Cauchy density in any dimension has Fourier transform $p(q) = \exp(-cq)$ (Feller, 1971). The d-dimensional Cauchy density is $C_d c/(c^2 + r^2)^{(d+1)/2}$: here, $C_1 = 1/\pi$, $C_2 = 1/2\pi$, and $C_3 = 1/\pi^2$. We now show that

> If the dispersal kernel is the Cauchy distribution with Fourier transform $p(q) = \exp(-cq)$, and if $d > 1$ the similarity function $F_d(r)$ is independent of r if $r \ll c$, while $F_2(r) \sim r^{1-d}$ if $r \gg c$.

The similarity function in d-dimensional space corresponding to the Cauchy kernel is

$$F_d(r) = C_d \frac{1 - F_d(0)}{\rho} \sum_{j=1}^\infty (1 - v)^j \frac{jc}{(r^2 + j^2 c^2)^{(d+1)/2}}. \tag{5.3}$$

If r is so small that $r^2 + c^2 j^2 \simeq c^2 j^2$ for those j contributing the overwhelming majority of the sum in (5.3), then

$$F_d(r) \simeq C_d \frac{1 - F_d(0)}{\rho} \sum_{j=1}^\infty \frac{(1 - v)^j}{j^d c^d}. \tag{5.4}$$

For these values of r, $F_d(r)$ depends very slightly on r and hardly at all on speciation rate v. For $r \gg c$, $F_d(r) \sim r^{1-d}$ (see Appendix A). When $d = 2$,

$$F_2(0) = \frac{\pi}{12c^2\rho + \pi} \tag{5.5}$$

and $F_2(r) \sim 1/r$ for large r. For arbitrary p in (5.1), the technique used in Appendix A to bound $F_2(r)$ for large r no longer works, but we conjecture that if $p < 1$, $F_2(r) \sim 1/r^{2p}$ for large r. In the two-dimensional case, the similarity function corresponding to the Cauchy kernel is compared with the similarity function corresponding to the Gaussian kernel in Fig. 1.

In the one-dimensional case

$$F_1(r) = \frac{c}{\pi\rho c + \ln(1/v)} \sum_{j=1}^\infty \frac{(1 - v)^j cj}{c^2 j^2 + r^2}, \tag{5.6}$$

$F_1(r)$ tends to a non-zero value for large r. Very crudely, for $d \geq 2$, the behavior of $F_d(r)$ with a Cauchy dispersal kernel tends to resemble the behavior of $F_{d+1}(r)$ with a Gaussian dispersal kernel. In the Cauchy case, $F_2(0)$ is independent of the speciation rate v and $F_2(r) \sim 1/r$ for large r as is true for $F_3(r)$ in the Gaussian case. In the Cauchy case, $F_1(0)$ depends on $\ln(1/v)$ in the same way

$F_2(0)$ does in the Gaussian case. On the other hand, $F_1(r)$ in the Cauchy case behaves very differently from $F_2(r)$ in the Gaussian case.

6. VOTER MODEL AND THE NO SPECIATION LIMIT

Now let us consider the limit as the speciation rate approaches zero. When $\sigma < \infty$, the diffusion approximation (3.10) applies in which $\Delta F(r) = 0$ when $v = 0$. Here, the only stable solution is $F(r) = C$. Equation (2.5) shows that $C = 1$. This implies that a single species must eventually take over the whole forest. Sawyer (1977b) describes the process by which ever larger monospecific patches grow when there is no speciation. If, in a forest without speciation containing N trees, every tree were a different species at time $t = 0$, then, after a large number t of tree generations, the total number of species remaining would be $\sim N \ln(t)/t$. Moreover, for large t and large r

$$F_2(r) \sim 1 - \frac{\ln(\gamma r^2/\sigma^2)}{\ln(t)}, \tag{6.1}$$

where $\gamma \simeq 0.57722$ is Euler's constant (Cox and Griffeath, 1986, Eqs. (3.2) and (3.3)). Thus, if $\sigma < \infty$, $F_2(r)$ always converges to 1, but very slowly.

When $\sigma < \infty$, the change in $F(r)$ over time may be simulated using an analogy with the "voter model" (Holley and Liggett, 1975; Cox and Griffeath, 1986; Dornic *et al.*, 2001). In this model, a "voter" is located at each site of a square lattice. At the beginning, let each voter prefer a different candidate, and suppose that, at each timestep each voter randomly chooses one of his four nearest neighbors and adopts his preference. This model also represents a square lattice of trees where each dead tree is replaced by the young of one of his four neighbors (Bramson *et al.*, 1998).

This model is in turn formally equivalent to a model of coalescing random walks (Holley and Liggett, 1975; Liggett, 1985; Chave *et al.*, 2002), an equivalence that provided the basis for the coalescence theory in genetics (Kingman, 1982). At time t, the voter at site $\mathbf{x}$ has a preference passed on through exactly one source or antecedent, for every time $t - \tau < t$. Let $\mathbf{A_x}(\tau)$ be the position of this antecedent at time $t - \tau$, so that $\mathbf{A_x}(0) = \mathbf{x}$. This is a simple random walk, where the distance $\|\mathbf{A_x}(\tau) - \mathbf{A_x}(\tau + 1)\|_2$ travelled at each timestep is 1. As τ increases, $t - \tau$ decreases: these random walks travel backwards in time. If, at time $t = 0$, each voter prefers a different candidate, then the probability $F_2(\mathbf{x}, \mathbf{y}, t)$ that at time t the voters at $\mathbf{x}$ and $\mathbf{y}$ prefer the same candidate is the probability that their preferences were passed on from the same antecedent, which is the probability that, for some τ $\mathbf{A_x}(\tau) = \mathbf{A_y}(\tau)$. At the smallest such τ, the random walks of these sites "coalesce": that is to say, for all larger τ they are one walk because for these τ, the antecedent sources of both voter's preferences are the same. If we let the voter model represent a forest where at time $t = 0$ each tree is a different species, as mentioned above, then $F(\mathbf{x}, \mathbf{y}, t)$ is the probability that at time t the trees at $\mathbf{x}$ and $\mathbf{y}$ are the same species.

If preferences are passed on faithfully (no speciation), the voter model predicts that, for systems in one and two dimensions, one preference will eventually prevail, while in three and more dimensions, different preferences coexist indefinitely (Holley and Liggett, 1975) for exactly the same reason that different random walks almost surely meet, given time enough, in one and two dimensions, but not in three or more (Feller, 1971).

If at time 0, each of N voters in a square lattice has a different preference, the mean time τ needed for one preference to spread to all N is $2N(\ln(N))^2/\pi$ (Cox, 1989). If, at time 0, a proportion p_s of the N voters prefer candidate s, then the time τ required for one preference to spread to all N is (Cox, 1989):

$$\tau \simeq \frac{2H_S}{\pi} N \ln(N), \qquad H_S = -\sum_{s=1}^{S} p_s \ln(p_s). \tag{6.2}$$

Here, H_S is the "entropy" of the initial state.

If σ is infinite, then if $v > 0$ the solution of Eq. (5.3) is the unique stable solution of Eq. (2.5). If $v = 0$, however, the solution of Eq. (5.3) still exists, but it is unstable. The only stable solution is $F_2(r) = 1$, yet, unlike the case where σ is finite, diversity may persist indefinitely.

7. NUMERICAL EXPERIMENTS

The formulas derived in Sections 2–5 applied to systems of infinite extent. Real systems, however, are finite. Cox's theorem (Eq. (6.2)) shows that when $v = 0$, the time required for one species to take over the forest depends on the forest's size and initial species composition. If $v > 0$, the finiteness of a forest may affect the similarity function $F(r)$ in various ways. Here, we use numerical simulations to address these questions (see also Harada *et al.*, 1997).

To simulate Hubbell's neutral model with dispersal limitation, we consider, with Durrett and Levin (1996), a

forest of $N = L^2$ trees on a square lattice where, at each elementary timestep:

(1) a tree chosen at random, without regard to its species, dies;
(2) the dead tree is immediately replaced by a young of one of its neighbors;
(3) with probability $2\pi P(r)r\,dr$, the distance from the newly dead tree to its replacement's seed–parent is between r and $r + dr$, where $P(r)$, the dispersal kernel, is the same for trees of all species, and
(4) with probability v, the replacement is a mutant of an entirely new species.

A Monte Carlo (MC) timestep is defined to be one tree generation, or $N = L^2$ elementary timesteps. During one MC timestep, each site experiences an average of one tree-death apiece. Young trees grow up only in the sites of their dead elders, thereby avoiding the tendency characteristic of continuous models for individuals to pile up at particular points, as remarked upon by Felsenstein (1975).

We run simulations on a 1024×1024 square lattice (N sites), with free boundary conditions. A square lattice of this size is large enough to avoid strong boundary effects, as verified by a few simulations on a square lattice of size 2048×2048. We vary both the speciation rate v and the shape of the dispersal kernel $P(r)$. For each choice of v and $P(r)$, we run 50–200 replicates to assess the sample-to-sample variance. We evaluate the similarity function $F(r)$ for each replicate as follows. When equilibrium is attained (see below), we draw $100N \simeq 10^8$ pairs of individuals at random from the lattice and ask whether they are conspecific. The maximum distance between members of a pair is 1448 cell units.

We actually simulate the random walk version of the voter model. The system starts at pseudo-time $\tau = 0$ with one random walk per site. Each random walk moves once on average during a MC timestep. Random walks always merge upon encounter. A speciation event represents the annihilation of a random walk (Bramson *et al.*, 1998; Chave *et al.*, 2002): by definition, the first representative of a new species has no conspecific ancestor. All the walks that had previously coalesced with the annihilated walk define a set of sites (the initial positions of these random walks) to which we affix a species label. We run simulations until all random walks have either coalesced, or suffered annihilation. At this time, every site in the lattice has a species label, and we call such a configuration an equilibrium distribution of species. In the random walk algorithm, one timestep corresponds to two timesteps of the direct version. Thus,
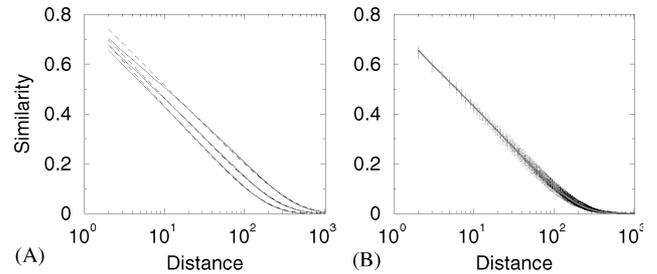

FIG. 2. Similarity function $F(r)$ in the neutral model with nearest-neighbor dispersal, in log-linear axes. The function $F(r)$ is drawn up to $L/2 = 512$ space units. Panel A: similarity function averaged over 50 runs for three different speciation rates as in Table 1 ($v = \theta/N$, $\theta = 4, 8, 16$, from right to left, $N = 1024^2$). Dashed lines correspond to the function $cK_0(x/\xi)$ plotted for the values of c and ξ corresponding to the above values of θ. This solution agrees fairly well for $r > \sigma$, but not for $r < \sigma$, as discussed in the text. Panel B: similarity functions for each of the 50 runs and for $\theta = 16$ (dots), and running average.

the effective parameter σ^2 of the dispersal kernel we use in the analytical formulas of the similarity function should be multiplied by 2. Indeed, the 2-step dispersal kernel is the self-convolution of the 1-step dispersal kernel, therefore, its variance of the 2-step dispersal kernel is just twice the variance of the 1-step dispersal kernel. Attaining equilibrium takes longer, the lower the speciation rate v. When $v = 3.81 \times 10^{-6}$ average time to equilibrium is 10^6 MC time steps, about $2/v$ generations. Our simulations take no more than a few minutes per replica on a powerful PC.

Let dead trees be replaced only by young of their four nearest neighbors. Let the distance between lattice points be 1, so $\rho = 1$. We compare the model's predictions with the similarity function $F(r)$ averaged over 50 replicate runs using the nearest-neighbor dispersal kernel. Since $\sigma = 1$, we expect Eq. (4.7) to fit the data for all r large enough that the discrepancy between a Gaussian dispersal kernel and the nearest-neighbor kernel ceases to affect $F(r)$. According to (4.7), if $\rho = 1$, $F(r) = cK_0(r/\xi)$ where the coefficient c is $2/(2\pi\sigma^2 + \ln(1/v) + C_0)$ and the correlation length ξ is $\sqrt{\sigma^2/(2v)}$. The correspondence between the predicted values of ξ and c, and those fitted from our simulated $F(r)$ (Fig. 2) are in agreement with theoretical prediction (Table 1). Replicate runs vary remarkably (Fig. 2, right panel), and the standard deviation is greatest for small speciation rates v (results not shown). For $v = 3.81 \times 10^{-6}$, the maximal relative standard deviation around the similarity is ~ 0.03.

We also test our model's predictions against simulations for the nearest we can come to a Gaussian dispersal kernel on a square lattice (Fig. 3), assuming

TABLE I

Comparisons between Predicted Values of ξ and c and Those Found by Fitting $cK_0(r/\xi)$ to $F(r)$ from Simulations with Different Speciation Rates $v = \theta/N$ and Dispersal Parameters σ ($N = 1024 \times 1024$)

v	σ^2	Observed S	Observed c	Predicted c	Observed ξ	Predicted ξ
3.81×10^{-6}	1	121	0.147	0.128	341	362
7.63×10^{-6}	1	222	0.150	0.134	215	256
1.53×10^{-5}	1	394	0.162	0.141	142	181
1.53×10^{-5}	2	264	0.121	0.115	239	256
1.53×10^{-5}	4	221	0.0953	0.0845	345	362
1.53×10^{-5}	8	198	0.0636	0.0552	585	512
1.53×10^{-5}	16	184	0.0390	0.0326	1295	724
3.05×10^{-5}	4	405	0.0970	0.0871	220	256
6.10×10^{-5}	8	670	0.0644	0.0574	215	256
1.22×10^{-4}	16	1165	0.0385	0.0337	209	256

Note. The mean number of species in the system, S, is also provided. The first three lines correspond to runs with the nearest-neighbor dispersal kernel (Fig. 2). The last seven lines correspond to runs with the Gaussian dispersal kernel (Fig. 3). To compute predicted values of c, we assumed that $C_0 = 0$.
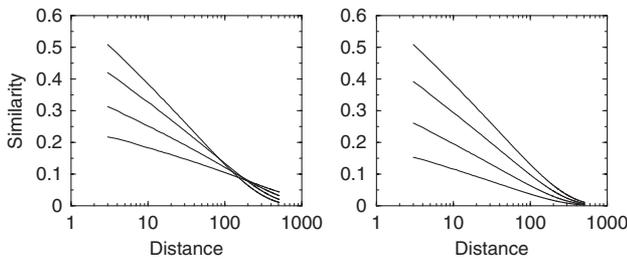

FIG. 3. Similarity function in the neutral model with Gaussian dispersal, and $v = \theta/N$ ($N = 1024^2$), averaged over 200 replicates in each case. The function $F(r)$ is drawn up to $L/2 = 512$ space units. Left panel: simulations with $\theta = 16$ and $\sigma^2 = 2, 4, 8$, and 16 (from top to bottom). Right panel: simulations such that the predicted value for the correlation length ξ is held constant at $\xi = 256$; both θ and σ^2 are varied: $\{\theta, \sigma^2\} = \{16, 1\}, \{32, 2\}, \{64, 4\}$, and $\{128, 8\}$ (from top to bottom). Observed ξ (the cross-over point between linear and convex shape in the panel) is roughly constant (see also Table 1).

that the probability of a young replacing its seed parent is 0. We vary θ between 4 and 128, and σ^2 between 2 and 16, with 200 replicates for each case. Predicted values of ξ underestimate the observed value only when ξ is larger than the system size (Table 1). Otherwise, our simulation's results agree with theoretical predictions.

8. DISCUSSION

We have calculated and simulated the probability $F(r)$ that two trees separated by a distance r are the same species, assuming competitive equivalence, limited seed dispersal, and balance between speciation and extinction. We have learned how $F(r)$ declines with increase of distance between the trees compared, and what factors affect the speed of decline. The behavior of $F(r)$ depends on the dimensionality of the system. For a one-dimensional system, and presumably, for a long, very narrow river-side gallery forest, $F(r)$ declines more slowly with r than in a forest extending in two dimensions. Moreover, if seeds are distributed about their parent tree according to a "fat-tailed" Cauchy distribution, in which a few seeds travel very great distances, rather than a Gaussian distribution, it is as if the forest extended in an extra dimension. In a forest with Cauchy seed dispersal, $F_2(r) \sim 1/r$ for large r, whereas in a similar forest with Gaussian seed dispersal $F_2(r) \sim 1/\sqrt{r} \exp(-r/\xi)$, where ξ is the correlation length. Spatially explicit, individual-based simulations show great variation among runs in $F(r)$, suggesting that testing this theory experimentally will require vast amounts of data (Rousset, 2000).

8.1. The Similarity Function and β-Diversity

Condit *et al.* (2002) and Leigh *et al.* (in press) measured β-diversity by the slope of $F(r)$ when plotted against $\ln(r)$, as a crude measure of species turnover, the rate at which species known from an area of forest disappear, and other species appear, as the species composition of progressively more distant areas is compared with that of the initial one. Unfortunately, $F(r)$ is a crude measure of species turnover, or β-

diversity, for the same reason $F(0)$ is a crude measure of α-diversity, the diversity of species coexisting in one region. Indeed, both depend disproportionately on the more common species, whereas turnover may be more rapid among rarer species (Pitman *et al.*, 2001). For example, in 1985, one randomly chosen hectare in BCI's 50-ha plot had 93 species among its 456 trees $\geqslant 10$ cm dbh, and $F(0) = 0.02562$. If the hectare's 29 species with one tree apiece were absent, there would be 64 species among 427 trees and its $F(0)$ would be 0.02548, only a 5.4% decrease, but the species number would drop by 31%.

The neutral theory has been compared with data from networks of plots in western Amazonia and central Panama (Condit *et al.*, 2002). In Amazonian Ecuador, setting $\sigma = 54.8$ m, $v = 3.6 \times 10^{-11}$ enabled the $F(r)$ given by Eq. (4.4) to fit observations rather well for $0.1 < r < 100$ km. When these Ecuadorian plots were compared with plots 1200 km distant in Amazonian Ecuador, however, $F(r)$ was far higher than predicted: some common species were so widespread that they must have been spread by natural selection (Condit *et al.*, 2002). In Panama, where spatial heterogeneity in climate and soil is much greater than in the upland forest of western Amazonia, setting $\sigma = 40.2$ m, $v = 4.8 \times 10^{-8}$, enabled Eq. (4.4) to fit the trend of the data for r between 0.2 and 50 km. The smaller σ required to fit the Panama data, and the greater scatter of these data about the trend, suggest that the influence of environmental heterogeneity on species turnover is greater in Panama (Condit *et al.*, 2002). The neutral theory of $F(r)$ suggested that speciation and limited dispersal influence species turnover and served Condit and his coworkers as a null hypothesis for distinguishing different influences on species turnover. Few other analyses of the decline in similarity of species composition between two plots with increased distance between them have yet been published, although Nekola and White (1999) provide one such analysis for boreal forest.

8.2. On the Relevance of the Neutral Theory

Despite its success in summarizing various arrays of empirical data (Hubbell, 2001; Condit *et al.*, 2002), the neutral model does not provide a perspicuous understanding of the causes of α-diversity in tropical trees. Indeed, this model's extraordinary capacity to match data is a spectacular warning of the dangers of inferring process from pattern.

The neutral model has no way of explaining the contrast between tropical and temperate-zone tree diversity (Leigh, 1999), or the difference in species

composition of floodplain and upland rainforest in Amazonia (Terborgh *et al.*, 1996; Pitman *et al.*, 1999). It ignores the trade-off between the ability to grow fast in large clearings and the ability to survive in deep shade (Brokaw, 1987), whereby the formation of light gaps allows pioneer tree species to persist in mature forest (Skellam, 1951; Denslow, 1987; Schnitzer and Carson, 2001).

Even for forest in homogeneous habitat, the assumption of the neutral model are implausible. The neutral model assumes a plant's fate is independent of its species, or those of its neighbors. Yet most seeds, seedlings and saplings are more likely to die when close to conspecifics, whether young or adult (Wills and Condit, 1999; Harms *et al.*, 2000). The neutral model assigns all species the same fecundity and the same mortality rate. However, Zhang and Lin (1997) and Yu *et al.* (1998) argued that differences in these parameters irrepairably falsified the neutral model. BCI's 50-ha plot has nine species with over 500 trees $\geqslant 10$ cm dbh. In five of these species, the number of trees changed far more between 1982 and 2000 than was consistent with the neutral theory (Condit *et al.*, 1995, 1996; R. Condit, pers. comm.).

On the other hand, null models can be extremely valuable for developing new theoretical approaches. Hubbell (1979, 1997) focussed salutary attention on the circumstance that α-diversity represents a balance between speciation or immigration and extinction. Can a neutral theory perform a similar service for β-diversity, by providing new mathematical approaches, or by viewing β-diversity as the joint effect of local speciation and limited dispersal?

Incorporating limited seed dispersal into ecological theory is an urgent challenge. Ribbens *et al.* (1994) evaluated the effect of differences among tree species in seed dispersal on a model of forest dynamics; Clark *et al.* (1999) fit mathematical formulae to observed dispersal kernels and showed how the dispersal kernel of a tree species might influence its capacity to spread. Several authors have already explored the implications of limited seed dispersal for the neutral model (Durrett and Levin, 1996; Hubbell, 2001; Chave *et al.*, 2002). The Gaussian dispersal kernel many theorists employ, however, is often inconsistent with observed seed shadows (Clark *et al.*, 1999). Moreover, different tree species disperse their seeds very different distances, according to very different kernels (Willson, 1993; Clark *et al.*, 1999; Muller-Landau, 2001), even though our neutral model assigns the same dispersal kernel to all trees. Finally, theorists can only solve the neutral model of β-diversity if $F(r)$ expresses an equilibrium between

speciation and extinction, an equilibrium that takes long to attain, of the order of $2/v$ tree generations, in the case of nearest-neighbor dispersal (Section 7, see also Maruyama, 1972). It is increasingly evident that for many tree species, "fat-tailed" dispersal kernels fit observed distributions of seeds about their parents better than Gaussian kernels do. Fat-tailed dispersal kernels may also hasten the approach to equilibrium, transforming neutral models into more practical null hypotheses.

More generally, the incorporation of Cauchy dispersal kernels may improve the usefulness of the models of isolation by distance now being used by many population geneticists. Relating the gene flow between different locales to the distance between these locales is a great challenge. Le Corre *et al.* (1997) have explored the influence of long-distance gene flow on the genetic structure of a tree population. Our analytical model could prove a useful null hypothesis for such investigations.

APPENDIX: TAIL OF THE SIMILARITY FUNCTION FOR THE CAUCHY DISPERSAL CURVE

In this appendix, we investigate the tail of F_d ($r \gg c$) in the case of a power-law dispersal curve of the Cauchy type (Eq. (5.3)). The approximation $r^2 + j^2c^2 \simeq j^2c^2$ is only valid if $j > r/c$. One can write

$$F_d(r) = \frac{C_d(1 - F_d(0))}{\rho c^d}\left(\sum_{j=1}^{r/c} \frac{j(1-v)^j}{((r/c)^2 + j^2)^{(d+1)/2}}\right.$$
$$\left. + \sum_{j=r/c}^{\infty} \frac{j(1-v)^j}{((r/c)^2 + j^2)^{(d+1)/2}}\right). \quad \text{(A1)}$$

In the first sum, the term $(1 - v)^j$ is dominant only when $r \sim c/v$. We do not consider these extremely long distances. We can, therefore, write

$$\frac{(r/c)(r/c + 1)}{2}\frac{1}{2^{(d+1)/2}(r/c)^{d+1}} < \sum_{j=1}^{r/c}\frac{j(1-v)^j}{((r/c)^2 + j^2)^{(d+1)/2}}$$
$$< \frac{(r/c)(r/c + 1)}{2}\frac{1}{(r/c)^{d+1}}. \quad \text{(A2)}$$

Since $r \gg c$

$$\frac{c^{d-1}}{2^{(d+3)/2}r^{d-1}} < \sum_{j=1}^{r/c}\frac{j(1-v)^j}{((r/c)^2 + j^2)^{(d+1)/2}} < \frac{c^{d-1}}{2r^{d-1}}. \quad \text{(A3)}$$

For the second sum, we also have

$$\sum_{j=r/c}^{\infty}\frac{(1-v)^j}{2^{(d+1)/2}j^d} < \sum_{j=r/c}^{\infty}\frac{j(1-v)^j}{((r/c)^2 + j^2)^{(d+1)/2}}$$
$$< \sum_{j=r/c}^{\infty}\frac{(1-v)^j}{j^d}. \quad \text{(A4)}$$

These series are uniformly convergent for $d > 1$. Therefore, we can approximate them as a sum from r/c to a very large number n, such that $n < r/c/v$. This proves that the term $(1 - v)^j$ can also be neglected from these series. Finally, we replace the summation term by its corresponding Riemann integral

$$\int_{u=r/c}^{\infty}\frac{1}{2^{(d+1)/2}u^d}\,du$$
$$< \sum_{j=r/c}^{\infty}\frac{j(1-v)^j}{((r/c)^2 + j^2)^{(d+1)/2}} < \int_{u=r/c}^{\infty}\frac{1}{u^d}\,du.$$

Consequently, if $d > 1$

$$\frac{1}{2^{(d+1)/2}}\frac{d+1}{2(d-1)}\frac{c^{d-1}}{r^{d-1}}$$
$$< \sum_{j=1}^{\infty}\frac{cj(1-v)^j}{((r/c)^2 + j^2)^{(d+1)/2}} < \frac{d+1}{2(d-1)}\frac{c^{d-1}}{r^{d-1}}$$

or

$$\frac{C_d(1 - F_d(0))}{\rho cr^{d-1}}\frac{d+1}{2^{(d+3)/2}(d-1)} < F_d(r)$$
$$< \frac{C_d(1 - F_d(0))}{\rho cr^{d-1}}\frac{d+1}{2(d-1)}. \quad \text{(A5)}$$

For a simpler proof of the same result, the sum in Eq. (5.3) can be approximated by an integral:

$$F_d(r) \simeq C_d\frac{1 - F_d(0)}{\rho}\int_{u=0}^{\infty}(1-v)^u\frac{jc}{(r^2 + u^2c^2)^{(d+1)/2}}$$
$$\simeq C_d\frac{1 - F_d(0)}{\rho}\int_{u=0}^{\infty}\frac{uc}{(r^2 + u^2c^2)^{(d+1)/2}}\,du$$

or

$$F_d(r) \simeq C_d\frac{1 - F_d(0)}{c\rho}\frac{1}{(d-1)r^{d-1}}. \quad \text{(A6)}$$

In the one-dimensional case, the first sum (A3) is

$$\frac{1}{4} < \sum_{j=1}^{r/c} \frac{j(1-v)^j}{((r/c)^2 + j^2)} < \frac{1}{2}$$

while, for the second sum (A5), we have

$$\frac{1}{2} \sum_{j=r/c}^{\infty} \frac{(1-v)^j}{j} < \sum_{j=r/c}^{\infty} \frac{j(1-v)^j}{((r/c)^2 + j^2)} < \sum_{j=r/c}^{\infty} \frac{(1-v)^j}{j}$$

which is a decreasing function of r, bounded from above by $\ln(1/v)$. We deduce that

$$\frac{C_1(1 - F_1(0))}{2\rho c}\left(\frac{1}{2} + \ln\left(\frac{1}{v}\right)\right) < F_1(r)$$
$$< \frac{C_1(1 - F_1(0))}{\rho c}\left(\frac{1}{2} + \ln\left(\frac{1}{v}\right)\right).$$

ACKNOWLEDGMENTS

REFERENCES

Ashton, P. S. 1964. "Ecological Studies in the Mixed Dipterocarp Forests of Brunei State," Oxford Forestry Memoirs, Clarendon press, Oxford.

Ashton, P. S. 1976. Mixed dipterocap forest and its variation with habitat in the Malayan lowlands: A re-evaluation at Pasoh, *Malay. For.* **39**, 56–72.

Ashton, P. S., and Hall, P. 1992. Comparisons of structure among mixed dipterocarp forests of northwestern Borneo, *J. Ecol.* **80**, 459–481.

Bramson, M., Cox, J. T., and Durrett, R. 1998. A spatial model for the abundance of species, *Ann. Probab.* **26**, 658–709.

Bramson, M., and Griffeath, D. 1980. Renormalizing the 3-dimensional voter model, *Ann. Probab.* **7**, 418–432.

Brokaw, N. V. L. 1987. Gap-phase regeneration of 3 pioneer tree species in a tropical forest, *J. Ecol.* **75**, 9–19.

Cavalli-Sforza, L. L., Menozzi, P., and Piazza, A. 1994. "The History and Geography of Human Genes," 541 pp. + 518 map pp., Princeton Univ. Press, Princeton, NJ.

Chave, J., Muller-Landau, H., and Levin, S. 2002. Comparing classical community models: Theoretical consequences for patterns of diversity, *Am. Nat.* **159**, 1–23.

Clark, J. S. 1998. Why trees migrate so fast: Confronting theory with dispersal biology and the paleorecord, *Am. Nat.* **152**, 204–224.

Clark, J. S., Fastie, C., Hurtt, G., Jackson, S. T., Johnson, C., King, G., and Lewis, M. 1998. Reid's paradox of rapid plant migration, *BioScience* **48**, 13–24.

Clark, J. S., Lewis, M., Horvath, L. 2001. Invasion by extremes: Population spread with variation in dispersal and reproduction, *Am. Nat.* **157**, 537–554.

Clark, J. S., Silman, M., Kern, R., Macklin, E., and HilleRisLambers, J. 1999. Seed dispersal near and far: Patterns across temperate and tropical forests, *Ecology* **80**, 1475–1494.

Condit, R. 1995. Research in large long-term tropical forest plots, *TREE* **10**, 18–22, 1995.

Condit, R. 1998. "Tropical Forest Census Plots," Springer, Berlin.

Condit, R., Hubbell, S. P. and Foster, R. B. 1992. Recruitment near conspecific adults and the maintenance of tree and shrub diversity in a neotropical forest, *Am. Nat.* **140**, 261–286.

Condit, R., Hubbell, S. P. and Foster, R. B. 1995. Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought, *Ecol. Monogr.* **65**, 419–439.

Condit, R., Hubbell, S. P. and Foster R. B. 1996. Changes in tree species abundance in a Neotropical forest: Impact of climate change, *J. Trop. Ecol.* **12**, 231–256.

Condit, R., Pitman, N., Leigh, E. G., Chave, J., Terborgh, J., Foster, R. B., Nuñez V., P., Aguilar, S., Valencia, R., Villa, G., Muller-Landau, H., Losos, E., Hubbell, S. P. 2002. Beta-diversity in tropical forest trees, *Science* **295**, 666–669.

Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees, *in* "Dynamics of Populations, Proceedings of the Advances Study Institute on Dynamics of Numbers of Populations" (P. J. den Boer and G. R. Gradwell, Eds.), pp. 298–312, Wageningen, Netherlands.

Cox, J. T. 1989. Coalescing random walks and voter model consensus times on the torus in Z^d, *Ann. Probab.* **17**, 1333–1366.

Cox, J. T., and Griffeath, D. 1986. Diffusive clustering in the 2-dimensional voter model, *Ann. Probab.* **14**, 347–370.

Crow, J. F., and Kimura, M. 1970. "An Introduction to Population Genetics Theory," Harper & Row, New York.

Davis, M. B. 1969. Climatic changes in southern Connecticut recorded by pollen deposition at Rogers Lake, *Ecology* **50**, 409–422

Denslow, J. S. 1987. Tropical treefall gaps and tree species diversity, *Annu. Rev. Ecol. Syst.* **18**, 431–451.

Dornic, I., Chaté, H., Chave, J., and Hinrichsen, H. 2001. Critical coarsening without surface tension: The voter universality class, *Phys. Rev. Lett.* **87**, 045,701–045,704.

Durrett, R., and Levin, S. 1996. Spatial models for species-area curves, *J. Theor. Biol.* **179**, 119–127.

Feller, W. 1971. "An Introduction to Probability Theory and its Applications," Wiley, New York.

Felsenstein, J. 1975. A pain in the torus: Some difficulties with models of isolation by distance, *Am. Nat.* **109**, 359–368.

Gentry, A. H. 1982. Patterns of neotropical plant species, *Evol. Ecol.* **15**, 1–84.

Gentry, A. H. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients, *Ann. Mo. Bot. Gard.* **75**, 1–34.

Givnish, T. J. 1999. On the causes of gradients in tropical tree diversity, *J. Ecol.* **87**, 193–210.

Gradshteyn, I. S., and Ryzhik, I. M. 2000. *In* "Tables of Integrals, Series and Products," (A. Jeffrey and D. Zwillinger, Eds.), 6th ed., 1163 pp., Academic Press, San Diego. [Formula numbers are the same in the 1980 editi on]

Harada, Y., Kawano, S., and Iwasa, Y. 1997. Probability of clonal identity: Inferring the relative success of sexual versus clonal reproduction from spatial genetic patterns, *J. Ecol.* **85**, 591–600.

Harms, K. E., Wright, S. J., Calderón, O., Hernández, A., and Herre, E. A. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest, *Nature* **404**, 493–495.

Holley, R. A., and Liggett, T. M. 1975. Ergodic theorems for weakly interacting infinite systems and the voter model, *Ann. Probab.* **3**, 643–663.

Horn, H. S. 1966. Measurement of "overlap" in comparative ecological studies, *Am. Nat.* **100**, 419–424.

Hubbell, S. P. 1979. Tree dispersion, abundance and diversity in a dry tropical forest, *Science* **203**, 1299–1309.

Hubbell, S. P. 1997. A unified theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs, *Coral Reefs* **16**, S9–S21.

Hubbell, S. P. 2001. "A Unified Neutral Theory of Biodiversity and Biogeography," Monographs in Population Biology, Princeton Univ. Press, Princeton, NJ, 448pp.

Hubbell, S. P., Condit, R., and Foster, R. B. 1990. Presence and absence of density dependence in a neotropical tree community, *Philos. Trans. R. Soc. London B* **330**, 269–281.

Hubbell, S. P., and Foster R. B. 1983. Diversity of canopy trees in a neotropical forest and implications for conservation, *in* "Tropical Rain Forest: Ecology and Management" (S. L. Sutton, T. C. Whitmore, and A. C. Chadwick, Eds.), pp. 25–41, Blackwell Scientific Publications, Oxford.

Hubbell, S. P, and Foster R. B. 1986. Canopy gaps and the dynamics of a neotropical forest, *in* "Plant Ecology" (M. J. Crawley, Ed.), pp. 77–96, Blackwell Scientific, Oxford.

Hubbell, S. P., Foster, R. B., O'Brien, S. T., Harms, K. E., Condit, R., Weschler, B., Wright, S. J., and Loo de Lao, S. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest, *Science* **283**, 554–557.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests, *Am. Nat.* **104**, 501–527.

Kimura, M. 1953. 'Stepping stone' model of population, *Annu. Rep. Nat. Inst. Genet. Japan* **3**, 62–63.

Kimura, M., and Ohta, T. 1971. "Theoretical Aspects of Population Genetics," Monographs in Population Biology, No. 4, Princeton Univ. Press, Princeton, NJ, 219pp.

Kimura, M., and Weiss, G. H. 1964. The stepping stone model of population structure and the decrease of genetic correlation with distance, *Genetics* **49**, 561–576.

Kingman, J. F. C. 1982. The coalescent, *Stochastic Proc. Appl.* **13**, 235–248.

Kot, M., Lewis, M. A., and van den Driessche, P. 1996. Dispersal data and the spread of invading organisms, *Ecology* **77**, 2027–2042.

Le Corre, V., Machon, N., Petit, R. J., and Kremer, A. 1997. Colonization with long-distance seed dispersal and genetic structure of maternally inherited genes in forest trees: A simulation study, *Genet. Res.* **69**, 117–125.

Leigh, E. G. 1999. "Tropical Forest Ecology. A View From Barro Colorado Island," Oxford Univ. Press, New York, Oxford, 245pp.

Leigh, E. G., Condit, R., and Loo de Lao, S. In press. Null models, sample plots, and tropical forest diversity, *in* "Tropical Forest Diversity and Dynamism: Findings from a Network of Large-Scale Forest Dynamics Plots." (E. C. Losos, R. Condit, J. V. LaFrankie, and E. G. Leigh, Eds.), Chicago Univ. Press, Chicago.

Leigh, E. G., Wright, S. J., Putz, F. E., and Herre, E. A. 1993. The decline of tree diversity on newly isolated tropical islands: A test of a null hypothesis and some implications, *Evol. Ecol.* **7**, 76–102.

Liggett, T. M. 1985. "Interacting Particle Systems," Springer, New York.

MacArthur, R. H., and Wilson, E. O. 1967. "The Theory of Island Biogeography," Princeton Univ. Press, Princeton, NJ.

Magurran, A. E. 1988. "Ecological Diversity and its Measurement," Princeton Univ. Press, Princeton, NJ, 179pp.

Malécot, G. 1948. "Les mathématiques de l'hérédité," Masson, Paris, 63pp. [English translation, "The Mathematics of Heredity," W. H. Freeman, New York, 1969, 88pp.]

Manokaran, N., LaFrankie, J. V., Kochummen, K. M., Quah, E. S., Klahn, J. E., Ashton, P. S., and Hubbell, S. P. 1990. Methodology for the fifty-hectare research plot at Pasoh Forest reserve, *Res. Pam. For. Res. Inst. Malaysia* **104**, 1–69.

Maruyama, T. 1972. Rate of decrease of genetic variability in a two-dimensional continuous population of finite size, *Genetics* **70**, 639–651.

Mayr, E. 1954. Change of genetic environment and evolution, *in* "Evolution as a Process" (J. Huxley, A. C. Hardy and E. B. Ford, Eds.), pp. 157–180, George Allen & Unwin, London.

Muller-Landau, H. C. 2001. "Seed dispersal: Empirical patterns, their origins, and consequences for community dynamics," Ph.D. Dissertation, Princeton Univ., Princeton, NJ.

Nagylaki, T. 1974. The decay of genetic variability in geographically structured populations, *Proc. Natl. Acad. Sci. USA* **71**, 2932–2936.

Nagylaki, T. 1976. The relation between distant individuals in geographically structured populations, *Math. Biosci.* **28**, 73–80.

Nekola, J. C., and White, P. S. 1999. The distance decay of similarity in biogeography and ecology, *J. Biogeogr.* **26**, 867–878.

Nei, M. 1987. "Molecular Evolutionary Genetics," Columbia Univ. Press, New York.

Okuda, T., Kachi, N., Yap, S. K., and Manokaran, N. 1997. Tree distribution pattern and fate of juveniles in a lowland tropical rainforest—implications for regeneration and maintenance of species diversity, *Plant Ecol.* **131**, 155–171.

Pitman, N. C. A., Terborgh, J., Silman, M. R., and Nuñez, P. 1999. Tree species distributions in an upper Amazonian forest, *Ecology* **80**, 2651–2661.

Pitman, N. C. A., Terborgh, J., Silman, M. R., Nuñez V., P., Neill, D., Ceron, C. E., Palacios, W. E., and Aulestia, M. 2001. Dominance and distribution of tree species in upper Amazonian terra firme forests, *Ecology* **83**, 2101–2117.

Pyke, C. R., Condit, R., Aguilar, S., and Lao, S. 2001. Floristic composition across a climatic gradient in a neotropical lowland forest, *J. Veg. Sci.* **12**, 553–566.

Ribbens, E., Silander, J. A., and Pacala, S. W. 1994. Seedling recruitment in forests: Calibrating models to predict patterns of tree seedling dispersion, *Ecology* **75**, 1794–1806.

Rousset, F. 2000. Genetic differentiation between individuals, *J. Evol. Biol.* **13**, 58–62.

Sawyer, S. 1976. Results for the stepping stone model for migration in population genetics, *Ann. Probab.* **4**, 699–728.

Sawyer, S. 1977a. Asymptotic properties of the equilibrium probability of density in a geographically structured population, *Adv. Appl. Probab.* **9**, 268–282.

Sawyer, S. 1977b. Rates of consolidation in a selectively neutral migration model, *Ann. Probab.* **5**, 486–493.

Schnitzer, S. A., and Carson W. P. 2001. Treefall gaps and the maintenance of species diversity in a tropical forest, *Ecology* **82**, 913–919.

Simpson, E. H. 1949. Measurement of diversity, *Nature* **163**, 688.

Skellam, J. G. 1951. Random dispersal in theoretical populations, *Biometrika* **38**, 196–218.

Terborgh, J., and Andresen, J. 1998. The composition of Amazonian forests: Patterns at local and regional scales, *J. Trop. Ecol.* **14**, 645–664.

Terborgh, J., Foster, R. B., and Nuñez V., P. 1996. Tropical tree communities: A test of the nonequilibrium hypothesis, *Ecology* **77**, 561–567.

Watterson, G. A. 1974. Models for the logarithmic species abundance distribution, *Theor. Popul. Biol.* **6**, 217–250.

Weiss, G. H., and Kimura, M. 1965. A mathematical analysis of the stepping stone model of genetic correlation, *J. Appl. Probab.* **2**, 129–149.

Whittaker, R. H. 1972. Evolution and measurement of species diversity, *Taxon* **21**, 213–251.

Wills, C., and Condit, R. 1999. Similar non-random processes maintain diversity in two tropical rainforests, *Proc. R. Soc. London B* **266**, 1445–11452.

Wills, C., Condit, R., Hubbell, S. P., and Foster, R. B. 1997. Strong density- and diversity-related effects help to maintain tree species diversity in a neotropical forest, *Proc. Natl. Acad. Sci. USA* **94**, 1252–1257.

Willson, M. F. 1993. Dispersal mode, seed shadows, and colonization patterns, *Vegetatio* **108**, 261–280.

Wright, S. 1931. Evolution in Mendelian populations, *Genetics* **16**, 97–159.

Wright, S. 1943. Isolation by distance, *Genetics* **28**, 114–138.

Wright, S. J. 2002. Plant diversity in tropical forests: A review of mechanisms of species coexistence, *Oecologia* **130**, 1–14.

Yu, D. W., Terborgh, J. W., and Potts, M. D. 1998. Can high tree species richness be explained by Hubbell's null model? *Ecology Lett.* **1**, 193–199.

Zhang, D.-Y., and Lin, K. 1997. The effects of competitive asymmetry on the rate of competitive displacement: How robust is Hubbell's community drift model? *J. Theor. Biol.* **188**, 361–367.