Insular Biogeographic Theory and Diffusion Models in Population Dynamics

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We examine a class of mathematical models describing the effects of habitat size and geometry on community structure. We deduce spatial effects at the community level from mechanistic models for the population dynamics and dispersal of individual populations together with some minimal hypotheses about the distribution of growth and dispersal rates among those populations. We use the models to deduce species–area curves, and in that sense they provide an alternative to the dynamic equilibrium theory of island biogeography introduced by MacArthur and Wilson. Since the models can explicitly incorporate various hypotheses about population dynamics and the nature and strength of interactions between species they permit a detailed analysis of how these hypotheses should affect community structure. We illustrate that point by contrasting the implications of different hypotheses in the context of refuge design. © 1994 Academic Press, Inc.

I. INTRODUCTION

A fundamental problem in biogeographic theory and refuge design is to determine how the size and geometry of insular habitats affect both population dynamics and community structure. Although previous theories have addressed the effects of habitat size and geometry on either population dynamics or community structure, there has not yet been a theoretical approach that integrates population level effects with community level effects. Population level effects have been examined theoretically in terms of reaction–diffusion equations as in (Skellam, 1951; Kierstead and Slobodkin, 1953; Okubo, 1980; Pacala and Roughgarden, 1982); see also the review articles (Levin, 1986; Kareiva, 1990). Community level effects have most frequently been examined from the viewpoint of the dynamic equilibrium theory of MacArthur and Wilson (1963, 1967) which together

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environmental heterogeneity into single species population models, as in (Cantrell and Cosner, 1989, 1991a, 1991b).

The types of communities we model are somewhat different from those for which dynamic equilibrium models of the MacArthur–Wilson type are most appropriate. We specifically consider the sort of relictual communities discussed in (Brown, 1971; Patterson and Atmar, 1986) which arise when a habitat island becomes isolated due to climatic or geological changes or habitat destruction. Such communities may be structured primarily by successive extinctions rather than by a balance between extinctions and colonizations. We consider two extreme cases: communities in which competition is assumed to play no role in community structure, and communities (perhaps more accurately termed guilds) in which competitive exclusion is a strong structuring factor. In the first case our modeling hypotheses suggest a species–area relation that is nonlinear under any standard transformation and which flattens out for very large areas. The species–area curve is qualitatively similar in that respect to those discussed in (Schoener, 1976; Gilpin and Armstrong, 1981; Gilpin and Diamond, 1981; Martin, 1981) in connection with the MacArthur–Wilson theory. In the second case our models yield the Gleason (1922) or logarithmic relation $S = \ln k + z \ln A$. This relation may be expressed in the equivalent form $e^S = kA^z$, which can be viewed as a power law with S replaced by its exponential e^S. (For that reason the Gleason relation is sometimes called exponential.)

II. The Models

Diffusion Models for Population Dynamics

Our modeling approach is to determine the number of species expected to coexist in a community occupying an isolated region such as an island by using models from population dynamics to decide whether a species with given rates of dispersal and per capita growth would persist or become extinct in the region, then using a distribution function reflecting the structure of a hypothetical community to count the number of species whose growth and dispersal rates lie in the range predicting persistence. To model population dynamics with spatial dispersal we use reaction–diffusion equations of the type introduced in (Skellam, 1951; Kierstead and Slobodkin, 1953) and applied in (Ludwig *et al.*, 1979; Pacala and Roughgarden, 1982; Murray and Sperb, 1983; Cantrell and Cosner, 1989, 1991a, 1991b). General discussions of modeling population dynamics with dispersal in terms of reaction–diffusion equations are given in (Okubo, 1980) and (Levin, 1986). Such models are very flexible and can be adapted to many many situations, but for the present purpose a rather simple with some assumptions about the relative numbers of rare and common species yields the species–area relation $S = CA^z$. In the present article we shall demonstrate that a synthesis of the two modeling approaches is possible and examine how such a synthesis sheds some new light on the "single large or several small reserves" (SLOSS) question in refuge design. Specifically, we show how a plausible theory of insular biogeography for certain types of communities may be deduced from diffusion models for the population dynamics of individual species and some simple hypotheses about the distribution of growth and dispersal rates among those species that might belong to the community. The most important aspect of our work is not the detailed analysis of the models themselves but the observation that spatially explicit models for population dynamics can provide a reasonable alternative to the MacArthur–Wilson approach to island biogeography, and in fact may give more insight into the mechanisms involved in structuring communities in some cases.

Our primary goal in this work is to develop and describe a method of connecting spatial effects at the hierarchal levels of population dynamics and community structure. To our knowledge there has been little work on that topic, although there seems to be some interest in the general question of how to move up and down through the hierarchy of individuals, populations, communities, and ecosystems. A recent paper of Holt (1992) suggests how metapopulation models can be used to understand certain aspects of island biogeography theory, but the focus is somewhat different than in the present article. Because our main purpose is to examine the connections between population dynamics and the theory of community structure in isolated habitats, we have used the simplest reasonable hypotheses about both the autecology of the species which constitute the community and about their interactions or the absence thereof. We recognize that in many cases the details of single species population dynamics are of critical importance. Refuges are often designed to protect a single species or a small number of species rather than a community or ecosystem. In view of that, much of our past work has dealt with the population dynamics of one or two species in complex environments; see (Cantrell and Cosner, 1989, 1991a, 1991b, 1993). We also recognize, however, that interactions between species can have profound and complicated effects on community structure. We therefore suggest some caution in the application to specific situations, especially those involving endangered species, of simple biogeographic theories such as those presented here or in the work of MacArthur and Wilson. We hope that the general approach of constructing models for the effects of habitat size and geometry on community structure from spatially explicit models for population dynamics can be expanded and refined in various ways. In particular, it should be possible to base a reasonable theory on metapopulation dynamics, as in (Holt, 1992), or to incorporate environmental heterogeneity into single species population models, as in (Cantrell and Cosner, 1989, 1991a, 1991b).

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$$\frac{\partial u}{\partial t}=d\left(\frac{\partial^2 u}{\partial x^2}+\frac{\partial u^2}{\partial y^2}\right)+ru+ug(u) \qquad \text{for} \quad (x, y)\in\Omega, t>0 \tag{1.1}$$

and

$$u(x, y, t)=0 \qquad \text{for} \quad (x, y)\in\partial\Omega. \tag{1.2}$$

In (1.1) the constants d and r are positive; d measures the rate of random dispersal of the population and r its intrinsic rate of increase at low densities in favorable habitats. The function $g(u)$ describes density-dependent effects, so we require $r+g(u)<0$ for u sufficiently large. This condition simply means that the net growth rate of the population becomes negative at high densities, reflecting limits on growth. In many cases $g'(u)<0$; for example, $g(u)=-u/K$ for the logistic equation with diffusion. We shall not require that assumption, but we will describe its implications. The boundary condition (1.2) reflects the hypothesis that the region surrounding Ω is utterly inhospitable. Thus, we assume that colonization is not a factor in the population dynamics on Ω. In principle our models could incorporate colonization; we plan to address that point in future work. For detailed discussions of the modeling leading to (1.1), (1.2) see (Skellam, 1951; Ludwig *et al.*, 1979; Okubo, 1980; Levin, 1986).

It has been known for some time that in models such as (1.1), (1.2) the existence of a positive equilibrium for the population density follows from the instability of the state with zero density; this observation is sometimes phrased "invasibility implies existence of a positive equilibrium." This result can be obtained via the methods of (Ludwig *et al.*, 1979) or (Cantrell and Cosner, 1989). Often mathematicians will assume that $g'(u)<0$ so that the equilibrium is unique, but this is not necessary; the condition $r+g(u)<0$ for large u is needed to prevent unbounded growth. (The situation is more complicated for systems involving direct interactions between species, as in diffusive Lotka–Volterra models, but often some form of persistence follows from invasibility; see (Pacala and Roughgarden, 1982; Hutson and Law, 1985; Cantrell and Cosner, 1993) for discussions. The stability or instability of the zero state is determined by the sign of the largest eigenvalue σ_1 for the problem

$$\begin{aligned} d\left(\frac{\partial^2\psi}{\partial x^2}+\frac{\partial^2\psi}{\partial y^2}\right)+r\psi=\sigma\psi \qquad & \text{in } \Omega \\ \psi=0 \qquad & \text{on } \partial\Omega. \end{aligned} \tag{1.3}$$

If $\sigma_1>0$ the zero state is unstable; that is, the population described by (1.1), (1.2) will increase at low densities. We shall view the quantities d and r as varying from species to species, so it is crucial to formulate the requirement $\sigma_1>0$ in terms of r and d.

The problem (1.3) can be solved explicitly in terms of the solution to

$$\begin{aligned} \frac{\partial^2\phi}{\partial x^2}+\frac{\partial^2\phi}{\partial y^2}+\lambda\phi=0 \qquad & \text{in } \Omega \\ \phi=0 \qquad & \text{on } \partial\Omega. \end{aligned} \tag{1.4}$$

The problem (1.4) has a smallest eigenvalue $\lambda_1(\Omega)$ which is characterized by having a positive eigenfunction ϕ_1. In (1.3), the largest eigenvalue is also characterized by a positive eigenfunction ψ_1. (For a detailed discussion of eigenvalue problems such as these, see (Courant and Hilbert, 1953).)

If we substitute $\psi_1=\phi_1$ from (1.4) into (1.3) and solve for σ_1 we obtain $\sigma_1=-d\lambda_1+r$ since

$$(-d\lambda_1+r)\,\phi_1=d\left(\frac{\partial^2\phi_1}{\partial x^2}+\frac{\partial^2\phi_1}{\partial y^2}\right)+r\phi_1=\sigma_1\phi_1,$$

so $\sigma_1>0$ if and only if

$$r/d>\lambda_1(\Omega). \tag{1.5}$$

We review the following result which is not original in this work but will be useful in our analysis.

THEOREM 1. *Suppose that $g(u)$ is a differentiable function with $g(0)=0$ and $r+g(u)<0$ for u sufficiently large. The problem* (1.1), (1.2) *has a positive equilibrium if* (1.5) *is satisfied. If in addition $g'(u)<0$, the problem* (1.1), (1.2) *has a unique globally stable positive equilibrium if and only if* (1.5) *holds.*

Discussion. Results corresponding to special cases of Theorem 1 are derived in (Skellam, 1951); more general results are derived in (Ludwig *et al.*, 1979; Cantrell and Cosner, 1989, 1991a, 1991b.) Even without the assumption $g'(u)<0$, (1.1) and (1.2) can be shown to predict permanence or uniform persistence for the population if (1.5) holds by the methods used for competition models in (Cantrell and Cosner, 1993); in general, if the condition $g'(u)<0$ does not hold then there may be multiple equilibria (Ludwig *et al.*, 1979).

Spatial Effects in Population Dynamics

The criterion (1.5) for the persistence of a species inhabiting Ω in terms of λ_1 makes it possible to study the effects of the geometry of Ω on the persistence of populations. The value of λ_1 is intimately related to the geometry of Ω. For example, of all regions with a given area, the circular disc has the smallest value of λ_1 (see, for example, (Bandle, 1980)) so that condition (1.5) can be satisfied with the weakest restrictions on r/d in that case. Results similar to Theorem 1 hold in the presence of environmental heterogeneity as described by a growth rate $r(x, y)$ depending on location; such results have been used to study the effects of heterogeneity in the articles (Pacala and Roughgarden, 1982; Cantrell and Cosner, 1989, 1991a, 1991b) among others. Our primary interest in the present article is in comparing homogeneous environments of different areas and perhaps different shapes. To that end we shall examine how λ_1 behaves when the region Ω is rescaled and we shall calculate the values of λ_1 for rectangular regions with different ratios of length to width. (The choice of rectangular regions is simply to illustrate the effects of shape in a situation where computations are simple.)

THEOREM 2. *Suppose that the region* Ω_0 *has area* 1 *and that* Ω *has the same shape as* Ω_0 *but has area* A. *If* λ_0 *is the principal eigenvalue for* (1.3) *on* Ω_0 *then the principal eigenvalue* $\lambda_1(\Omega)$ *for* (1.3) *on* Ω *is* λ_0/A. *Thus, the criterion* (1.5) *for persistence of the population described by* (1.1), (1.2) *becomes* $r/d > \lambda_0/A$.

Proof. To rescale Ω_0 to Ω we make the change of variables $\tilde{x} = \sqrt{A}\, x$, $\tilde{y} = \sqrt{A}\, y$. This preserves the shape of Ω_0 and gives it area A. The problem

$$\frac{\partial^2 \phi}{\partial \tilde{x}^2} + \frac{\partial^2 \phi}{\partial \tilde{y}^2} + \lambda \phi = 0 \qquad \text{in } \Omega$$

$$\phi = 0 \qquad \text{on } \partial\Omega$$

has a positive solution $\phi(\tilde{x}, \tilde{y})$ if and only if $\lambda = \lambda_1(\Omega)$. However, $(\tilde{x}/\sqrt{A}, \tilde{y}/\sqrt{A}) \in \Omega_0$ exactly when $(\tilde{x}, \tilde{y}) \in \Omega$, so $\phi_0(\tilde{x}/\sqrt{A}, \tilde{y}/\sqrt{A})$ is defined and positive on Ω and is zero on $\partial\Omega$. Using $x = \tilde{x}/\sqrt{A}$ and $y = \tilde{y}/\sqrt{A}$ we find that the problem rescales into a form which is equivalent to (1.3) on Ω with $\lambda = \lambda_0/A$. Since we have a solution for (1.3) on Ω with $\phi(\tilde{x}, \tilde{y}) = \phi_0(\tilde{x}/\sqrt{A}, \tilde{y}/\sqrt{A}) > 0$ on Ω, it follows that $\lambda_1(\Omega) = \lambda_0/A$.

In simple geometries it is often possible to find eigenvalues via the method of separation of variables. If Ω is a rectangle we can seek solutions to (1.4) of the form $\phi(x, y) = X(x)\, Y(y)$, so that the equation becomes $X''(x)\, Y(y) + X(x)\, Y''(y) + \lambda X(x)\, Y(y) = 0$ or $X''(x)/X(x) = -\lambda - (Y''(y)/Y(y))$. Since the expression on the left now depends on x and that on the right only on y, both must be constants. Hence $X'' = -(\lambda + \zeta)\, X$ and $Y'' = \zeta Y$ for some constants ζ and λ. These ordinary differential equations can then be solved explicitly. Only certain values of ζ and λ admit solutions that satisfy the boundary condition $\phi(x, y) = X(x)\, Y(y) = 0$, and only the smallest such value for λ admits positive solutions. That smallest value is λ_1. The method of separation of variables is discussed in most introductory texts on partial differential equations; a classical reference is (Courant and Hilbert, 1953). The method can be applied in other simple geometries; for example, circular sectors and annuli can be treated in this way if polar coordinates are used. If Ω is the unit square $\{(x, y): 0 \leqslant x \leqslant 1, 0 \leqslant y \leqslant 1\}$ it turns out that $\phi(x, y) = \sin(\pi x) \sin(\pi y)$ and $\lambda_1 = 2\pi^2$.

If Ω is a rectangle with area A and ratio of width to length w, the dimensions will be $\sqrt{A}/\sqrt{w} \times \sqrt{Aw}$. If we put our coordinate axis along the bottom and the left side of the rectangle we can write the eigenfunction as $\phi(x, y) = \sin(\pi \sqrt{w}\, x/\sqrt{A}) \sin(\pi y/\sqrt{Aw})$, so $\lambda_1 = \pi^2[w + (1/w)]/A$. In the general case the expression for λ_1 as λ_0/A allows the separation of shape from area and hence permits the analysis of area effects.

Derivation of Species–Area Relations

So far we have considered only the effects of the size and shape of Ω on the dynamics of a single population. To pass from these to a theoretical model for the number of species expected to occur in a community inhabiting Ω we must make some assumptions about the distribution of the parameter r/d relative to the community. (It would be of interest to examine data for real communities, but we are not aware of any source where such data are tabulated.) We shall examine two simple sets of hypotheses that are plausible descriptions of two different sorts of community structure. The first set of hypotheses is based on the assumption that the community consists of species that do not significantly limit each other via competition, that the parameter values for r/d are distributed along a continuum, and that any species that can persist will be represented in the community. In that case the number of species expected could be calculated by integrating the distribution function for the number of species relative to r/d over the range $r/d > \lambda_0/A$. The second set of hypotheses is based on the assumption that the community is highly structured by competitive exclusion. The question of the extent to which competition structures actual communities is controversial; see (Diamond, 1975b; Connor and Simberloff, 1979; Gilpin and Diamond, 1982, 1984, 1987; Wilson, 1987). We take no position on that question. Our modeling approach can be adapted to either extreme assumption about the role of competition and yields reasonable results in either case. The hypotheses we impose are simple prototypes and many others could be used instead.

Species–Area Relations: Communities without Competition

Suppose that the parameter r/d is allowed to vary continuously. To count the number of species with $r/d > \lambda_1/A$ we need a distribution function $s(p)$ so that the number of species with $p_1 < r/d < p_2$ is given by the integral of $s(p)$ from p_1 to p_2. In that case the number of species with $r/d > \lambda_0/A$ will be

$$s^*(A) = \int_{\lambda_0/A}^{\infty} s(p)\, dp. \tag{1.6}$$

The values of r and d for a given species are always positive and are likely to depend on the interaction of numerous factors. A typical factor might be size, which might be expected to correlate positively with d but negatively with r since larger animals will generally have lower birth rates but may be able to travel farther in unit time (see Bonner, 1965). Since r and d depend on many factors it is likely that there will be few species with very large or small values for r/d and many with intermediate values. A distribution function with that sort of qualitative behavior which gives a good description of the distribution of many biological quantities (see Ehrlich and Roughgarden, 1987, Chap. 19) is the lognormal distribution, and we shall use that for $s(p)$ in (1.6). We assume a species pool of S_0 species and obtain

$$S^*(A) = \frac{S_0}{\sqrt{2\pi}\,\sigma} \int_{\lambda_0/A}^{\infty} \frac{e^{-(\ln p - \mu)^2/2\sigma^2}}{p}\, dp, \tag{1.7}$$

where μ and σ are the usual parameters in the lognormal distribution. Other assumptions about $s(p)$ are certainly reasonable; in particular, the choice $s(p) = kp^{-(z+1)}$ would lead to the Arrhenius (1921) or power law form $S(A) = CA^z$. However, it is not clear why that choice would be any more or less appropriate than the lognormal distribution in this context. In fact, a choice of distribution function $s(p)$ with $\int_0^\infty s(p)\, dp$ finite might be preferred to choices where the integral is infinite since a finite integral reflects a finite pool of possible species. In the next section we shall examine how well (1.7) can be made to fit some of the data sets used in earlier biogeographic studies. In what follows we shall use $S^*(A)$ exclusively to designate the species–area curve defined in (1.7) via the lognormal distribution and $S(A)$ exclusively to designate the power law $S(A) = CA^z$.

Species–Area Relations: Communities with Competition

The idea of "limiting similarity" of species (or alternatively the idea that only a certain amount of niche overlap is possible if species are to coexist) is formulated quantitatively in (Hutchinson, 1959) and more theoretically in (May, 1973). If a collection of morphologically similar species complete for a type of food that occurs in varying sizes, a typical hypothesis would be that a pair of species occupying adjacent niches will differ in size by some constant factor. If size is measured by a linear dimension such as length, it has been suggested that the factor should be 1: 1.3; see (Roughgarden 1989, p. 204) for a discussion and references. Certainly that hypothesis is too simple for many real situations, but it can serve as a reasonable starting point for theoretical work. Let us then suppose that we have a community with limited membership, each of whose members occupies a niche corresponding to a certain size, with the possible sizes of species inhabiting adjacent niches differing by a constant factor. In such a community the parameters r and d would not take on all values, but only certain discrete values corresponding to the discrete niches. It is plausible that r may vary inversely with size while d may vary directly; see, for example, the discussion of size in (Bonner, 1965). Suppose that the parameters r and d associated with the niche corresponding to the smallest body size are $r = r_0$ and $d = d_0$. The parameters associated with the niche corresponding to the second smallest body size would then be $r = Pr_0$ and $d = Qd_0$ with constant factors $P < 1$ and $Q > 1$ describing the displacement between adjacent niches. For the third niche we should have $r = P(Pr_0) = P^2 r_0$ and $d = Q(Qd_0) = Q^2 d_0$, again because we assume that adjacent niches correspond to body sizes which differ by a constant factor. If we continue this process, the coefficients for the ith niche should be $r = P^i r_0$, $d = Q^i d_0$. If we let $R = P/Q$ then $R < 1$ and the critical parameter r/d corresponding to the ith niche will be $r/d = P^i r_0 / Q^i d_0 = R^i r_0/d_0$. The number of species to be expected in a region Ω with fixed shape and area A is then determined by finding the largest value of i for which the ratio r_0/d_0 multiplied by the ith power of R satisfies

$$R^i r_0/d_0 > \lambda_0/A. \tag{1.8}$$

Solving the corresponding equality for i in terms of A yields

$$i = [\log(\lambda_0 d_0/r_0) - \log A]/\log R. \tag{1.9}$$

We may interpret i as the number of species which can be expected in our community. Since $R < 1$, $\log R < 0$, so (1.9) may be rewritten as

$$S^{\#}(A) = \log k + z \log A, \tag{1.10}$$

where z is a positive constant. The expression (1.10) is a version of the Gleason (1922) or exponential law for species numbers relative to area. It is equivalent to the formulation $e^S = kA^z$, which is essentially the power law with S replaced by its exponential e^S. That law has been used to some extent and fits some data sets reasonably well. A historical discussion of the use of (1.10) and an extensive statistical analysis of (1.10) and the power law $S(A)=CA^z$ is given in (Conner and McCoy, 1979). Since they provide a fairly detailed discussion and analysis of (1.10) we shall only make the observation that (1.10) is a formulation which is at least plausible and has been used to some extent as an alternative to the more usual power law. We can make the shape dependence in (1.10) more precise by observing that $\log k=\log(\lambda_0 d_0/r_0)/\log R$.

Shape Effects in Species–Area Relations

Both (1.6) and (1.10) depend on λ_0. If we wish to examine shape effects, we can do so by observing how shape affects λ_0. For both (1.6) and (1.10), an increase in λ_0 yields a decrease in the projected number of species. Among all regions of unit area, the one with the smallest value of λ_0 is the circle (see (Bandle, 1980)). For a square, $\lambda_0=2\pi^2$; and as we have observed earlier, for a rectangle with width to length ratio w, $\lambda_0=\pi^2[w+(1/w)]$. It follows that in such a case we have

$$\lambda_0/A=\pi^2[w+(1/w)]/A. \tag{1.11}$$

Formula (1.11) suggests that variations in shape as measured by w should have the same degree of influence on S^* or $S^\#$ as does A. This appears to disagree with the statistical study (Blouin and Connor, 1985). However, an examination of the area and shape variations of insular habitats or islands in typical data sets (e.g., from (Preston, 1962) or from (Brown, 1971) indicates that within a data set area is likely to vary significantly more than shape. The montane "island" habitats discussed in (Brown, 1971) are mostly somewhat elongated; the oceanic islands in (Preston, 1962) are somewhat irregular but generally closer to being round, and so on. Also, our models do not incorporate colonization, so the boundary acts as a sink but not as a source. In this context it is to be expected that geometries with relatively short boundaries (such as circles) will be predicted to sustain the most species. If colonization is an important factor, then the boundary will act as a source as well and the expected effects of shape variation may be very different; see, for example, the comments in (Connor and McCoy, 1979).

III. EMPIRICAL EVIDENCE FOR NEW SPECIES–AREA RELATIONS IN THE ABSENCE OF COMPETITION

In this section we briefly consider how well the formula for $S^*(A)$ given in (1.7) fits some data sets. Most of the data sets we consider are taken from (Preston, 1962) and were used in the early development of island biogeography theory by MacArthur and Wilson (1963, 1967). We also consider the data from (Brown, 1971); those data arise from a situation that Brown describes as "nonequilibrium insular biogeography" in which colonization is argued to be of negligible importance. We have ignored shape effects; the "islands" are assumed to be square, so that $\lambda_0=2\pi^2$. If the additional parameter w discussed in Section 1 to describe shape is also used, it should be possible to improve the fit somewhat, but we have not attempted that. The object is not to validate statistically the theory we have presented, but only to show that on the basis of fitting data sets the theory is plausible. We note that the formulation for $S^*(A)$ in (1.7) involves three parameters rather than the two involved in the power law relation $S(A)=CA^z$, so we should expect $S^*(A)$ to perform at least as well as $S(A)$. In a sense, the main point of this article is to provide a method for incorporating as many biologically relevant parameters as desired into the species–area relation. If the simple diffusion model in (1.1), (1.2) were replaced by the more complex and detailed models of the sort described in (Cantrell and Cosner 1989, 1991a, b) it should be possible to incorporate parameters that describe environmental heterogeneity, directed motion or migration as well as random diffusion, and the degree of hostility of the exterior of the insular habitats under consideration, since all of those factors influence the eigenvalue λ_0 in more or less quantifiable ways.

We have fitted the species–area curves both to untransformed data and to log transformed data. It is not clear to us whether it is more appropriate to fit the relation (1.7) defining $S^*(A)$ to the untransformed data or to the log transformed data since the relation remains nonlinear under any standard transformation of data. However, it has been standard practice to fit the power law relation $S(A)=CA^z$ to log transformed data; that is natural since the power law becomes linear in log–log plots. In fitting both untransformed and log transformed data we used the method of least squares. For an untransformed data set consisting of n species–area pairs (s_i, a_i) we minimized the error E given by the expressions

$$E=\sum_{i=1}^{n}[S^*(S_0,\mu,\sigma,a_i)-s_i]^2 \tag{2.1}$$

for $S^*(A)$ as defined in (1.7) and

$$E=\sum_{i=1}^{n}[S(C,z,a_i)-s_i]^2 \tag{2.2}$$

for $S(A)=CA^z$ relative to (S_0,μ,σ) and (C,z) respectively. As an additional test for goodness of fit we computed the coefficient of determination,

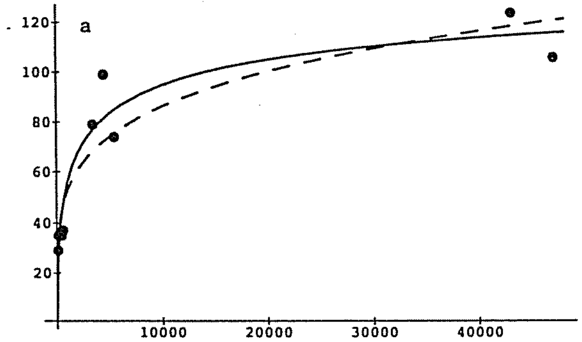

FIG. 1a. Birds of the West Indies. The abscissa represents area; the ordinate represents the number of species. The data points are taken untransformed from (Preston, 1962, Table IV). The solid curve is the graph of $S^*(A)$, as defined in (1.7), fitted to the untransformed data by minimization of the least squares error (2.1). The broken curve is the graph of $S(A)=CA^z$, also fitted to the untransformed data by minimization of the least squares error (2.2). The computed values of the parameters in $S^*(A)$ and $S(A)$ and of the goodness of fit are as follows: for S^*, $S_0=140$, $\mu=-5.45$, $\sigma=3.18$, least squares error $E=857$, coefficient of determination $(r^2)=0.930$; for S, $C=11.6$, $z=0.218$, least squares error $E=1300$, coefficient of determination $(r^2)=0.894$.

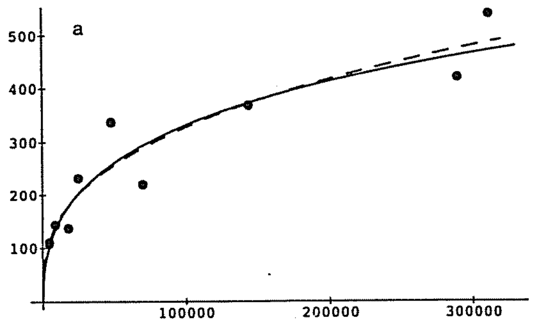

FIG. 2a. Birds of the East Indies. The abscissa represents area; the ordinate represents the number of species. The data points are taken untransformed from (Preston, 1962, Table V). The solid curve is the graph of $S^*(A)$, as defined in (1.7), fitted to the untransformed data by minimization of the least squares error (2.1). The broken curve is the graph of $S(A)=CA^z$, also fitted to the untransformed data by minimization of the least squares error (2.2). The computed values of the parameters in $S^*(A)$ and $S(A)$ and of the goodness of fit are as follows: for S^*, $S_0=2200$, $\mu=-14.1$, $\sigma=4.72$, least squares error $E=20,900$, coefficient of determination $(r^2)=0.895$; for S, $C=5.96$, $z=0.348$, least squares error $E=20,300$, coefficient of determination $(r^2)=0.897$.

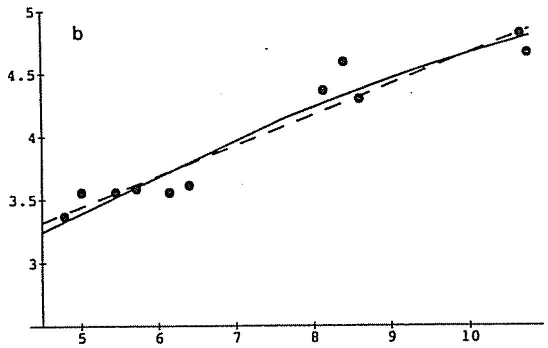

FIG. 1b. Birds of the West Indies. The abscissa represents log (area); the ordinate represents log (number of species). The data points are taken from (Preston, 1962, Table IV), but are log–log transformed. The solid curve is the log–log graph of $S^*(A)$, where $S^*(A)$ is defined in (1.7). The broken line is the log–log graph of $S(A)=CA^z$; thus C is the y-intercept and z is the slope. The curves were fitted to the data (after a logarithmic transformation) by minimization of the (logarithmic) least squares error $\bar{E}$ given for $S^*(A)$ in (2.3) and for $S(A)$ in (2.4). The coefficient of determination was computed in terms of the logarithmically transformed data and relations. The computed values of the parameters in $S^*(A)$ and $S(A)$ and of the goodness of fit are as follows: for S^*, $S_0=280$, $\mu=-9.42$, $\sigma=5.4$, (logarithmic) least squares error $\bar{E}=0.211$, (logarithmic) coefficient of determination $(r^2)=0.930$; for S, $C=9.20$, $z=0.244$, (logarithmic) least squares error $\bar{E}=0.235$, (logarithmic) coefficient of determination $(r^2)=0.922$.

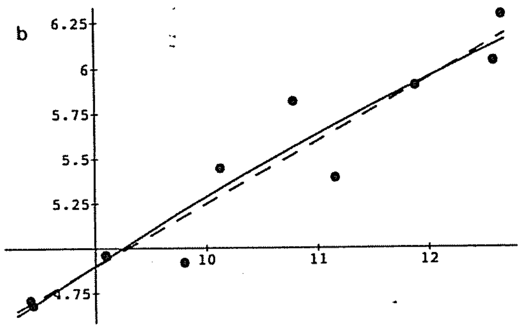

FIG. 2b. Birds of the East Indies. The abscissa represents log (area); the ordinate represents log (number of species). The data points are taken from (Preston, 1962, Table V), but are log–log transformed. The solid curve is the log–log graph of $S^*(A)$, where $S^*(A)$ is defined in (1.7). The broken line is the log–log graph of $S(A)=CA^z$; thus C is the y-intercept and z is the slope. The curves were fitted to the data (after a logarithmic transformation) by minimization of the (logarithmic) least squares error $\bar{E}$ given for $S^*(A)$ in (2.3) and for $S(A)$ in (2.4). The coefficient of determination was computed in terms of the logarithmically transformed data and relations. The computed values of the parameters in $S^*(A)$ and $S(A)$ and of the goodness of fit are as follows: for S^*, $S_0=2830$, $\mu=-15.5$, $\sigma=5.28$, (logarithmic) least squares error $\bar{E}=0.281$, (logarithmic) coefficient of determination $(r^2)=0.908$; for S, $C=5.69$, $z=0.351$, (logarithmic) least squares error $\bar{E}=0.274$, (logarithmic) coefficient of determination $(r^2)=0.910$.

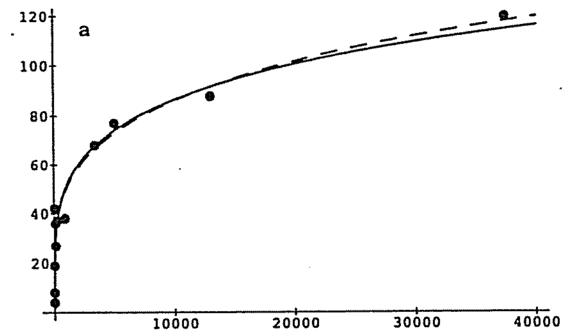

FIG. 3a. Land Vertebrates on Islands in Lake Michigan. The abscissa represents area; the ordinate represents the number of species. The data points are taken untransformed from (Preston, 1962, Table VI). The solid curve is the graph of $S^*(A)$, as defined in (1.7), fitted to the untransformed data by minimization of the least squares error (2.1). The broken curve is the graph of $S(A)=CA^z$, also fitted to the untransformed data by minimization of least squares error (2.2). The computed values of the parameters in $S^*(A)$ and $S(A)$ and of the goodness of fit are as follows: for S^*, $S_0=1770$, $\mu=-22.4$, $\sigma=9.42$, least squares error $E=531$, coefficient of determination $(r^2)=0.959$; for S, $C=9.64$, $z=0.238$, least squares error $E=514$, coefficient of determination $(r^2)=0.961$.

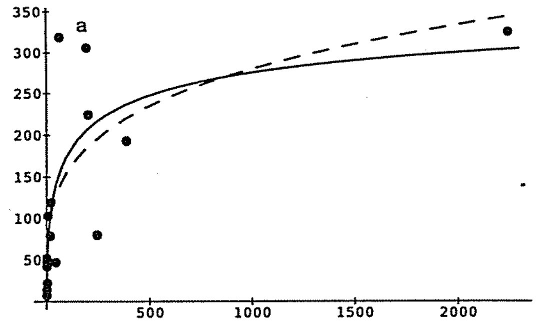

FIG. 4a. Land plants of the Galapagos. The abscissa represents area; the ordinate represents the number of species. The data points are taken untransformed from (Preston. 1962, Table VII). The solid curve is the graph of $S^*(A)$, as defined in (1.7), fitted to the untransformed data by minimization of the least squares error (2.1). The broken curve is the graph of $S(A)=CA^z$, also fitted to the untransformed data by minimization of least squares error (2.2). The computed values of the parameters in $S^*(A)$ and $S(A)$ and of the goodness of fit are as follows: for S^*, $S_0=380$, $\mu=-2.63$, $\sigma=3.33$, least squares error $E=73,200$. coefficient of determination $(r^2)=0.627$; for S, $C=48.4$, $z=0.254$, least squares error $E=77,900$, coefficient of determination $(r^2)=0.604$.

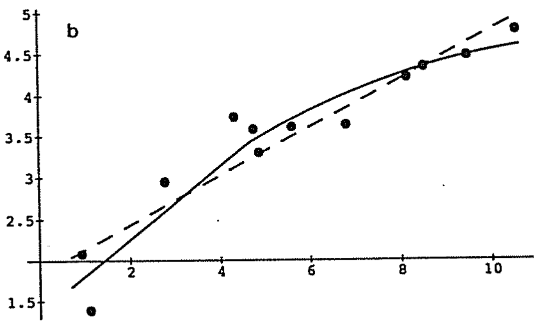

FIG. 3b. Land Vertebrates on Islands in Lake Michigan. The abscissa represents log (area); the ordinate represents log (number of species). The data points are taken from (Prestion 1962, Table VI), but are log–log transformed. The solid curve is the log–log graph of $S^*(A)$, where $S^*(A)$ is defined in (1.7). The broken line is the log–log graph of $S(A)=CA^z$; thus C is the y-intercept and z is the slope. The curves were fitted to the data (after a logarithmic transformation) by minimization of the (logarithmic) least squares error $\tilde{E}$ given for $S^*(A)$ in (2.3) and for $S(A)$ in (2.4). The coefficient of determination was computed in terms of the logarithmically transformed data and relations. The computed values of the parameters in $S^*(A)$ and $S(A)$ and of the goodness of fit are as follows: for S^*, $S_0=124$, $\mu=-5.00$, $\sigma=3.85$, (logarithmic) least squares error $\tilde{E}=0.837$, (logarithmic) coefficient of determination $(r^2)=0.922$; for S, $C=6.31$, $z=0.295$, (logarithmic) least squares error $\tilde{E}=1.30$, (logarithmic) coefficient of determination $(r^2)=0.879$.

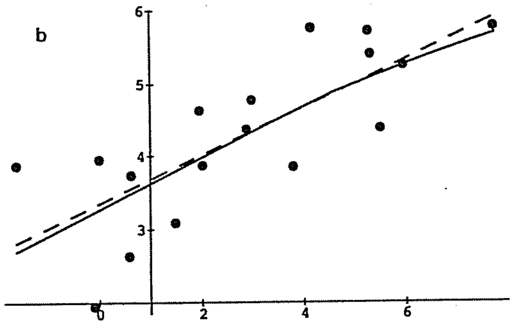

FIG. 4b. Land plants of the Galapagos. The abscissa represents log (area); the ordinate represents log (number of species). The data points are taken from (Preston, 1962, Table VII), but are log–log transformed. The solid curve is the log–log graph of $S^*(A)$, where $S^*(A)$ is defined in (1.7). The broken line is the log–log graph of $S(A)=CA^z$; thus C is the y-intercept and z is the slope. The curves were fitted to the data (after a logarithmic transformation) by minimization of the (logarithmic) least squares error $\tilde{E}$ given for $S^*(A)$ in (2.3) and for $S(A)$ in (2.4). The coefficient of determination was computed in terms of the logarithmically transformed data and relations. The computed values of the parameters in $S^*(A)$ and $S(A)$ and of the goodness of fit are as follows: for S^*, $S_0=1600$, $\mu=-11.2$, $\sigma=6.42$, (logarithmic) least squares error $\tilde{E}=8.40$, (logarithmic) coefficient of determination $(r^2)=0.573$; for S, $C=28.6$, $z=0.331$, (logarithmic) least squares error $\tilde{E}=8.17$, (logarithmic) coefficient of determination $(r^2)=0.585$.

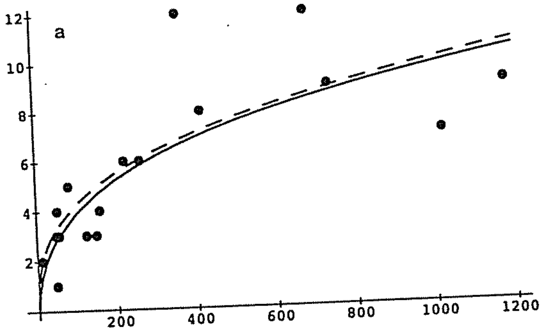

FIG. 5a. Mammals in montane isolates, western U.S. The abscissa represents area; the ordinate represents the number of species. The data points are taken untransformed from (Brown, 1971, Table 1). The solid curve is the graph of $S^*(A)$, as defined in (1.7), fitted to the untransformed data by minimization of the least squares error (2.1). The broken curve is the graph of $S(A)=CA^z$, also fitted to the untransformed data. The computed values of the parameters in $S^*(A)$ and $S(A)$ and of the goodness of fit are as follows: for S^*, $S_0=10.6$, $\mu=-2.72$, $\sigma=1.46$, least squares error $E=54.9$, coefficient of determination $(r^2)=0.697$; for S, $C=0.793$, $z=0.366$, least squares error $E=64.3$, coefficient of determination $(r^2)=0.644$. Since one of the habitat supports 12 species, we recomputed the coefficients for S^* with S_0 set equal to 12. That computation yielded $\mu=-3.03$, $\sigma=1.78$ with $E=55.6$ and $r^2=0.692$.

r^2, for the fitted curves relative to the untransformed data. For the corresponding log transformed data set $(\log s_i, \log a_i)$ we fitted the curves by minimizing the expressions

$$\tilde{E}=\sum_{i=1}^{n}[\log S^*(S_0, \mu, \sigma, a_i)-\log s_i]^2 \tag{2.3}$$

for $S^*(A)$ defined in (1.7) and

$$\begin{aligned}\tilde{E}&=\sum_{i=1}^{n}[\log S(C, z, a_i)-\log s_i]^2\\&=\sum_{i=1}^{n}[\log C+z\log a_i-\log s_i]^2\end{aligned} \tag{2.4}$$

for $S(A)=CA^z$ relative to (S_0, μ, σ) and (C, z), respectively. We also computed the coefficient of determination (r^2) relative to the log transformed data. The computations were performed in Mathematica on a Macintosh IIcx. Different sorts of fitting techniques may yield different results. It is interesting to note that in some early studies (e.g., Preston (1962)), data are fitted "by eye" from log–log plots. We observe that some of the computations for $S^*(A)$ yield what seem to be unrealistically high values for the parameter S_0 describing the total number of species available as potential community members.

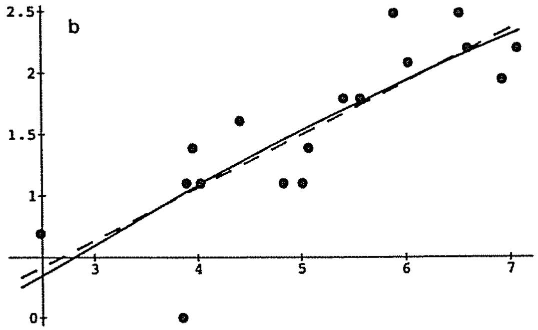

FIG. 5b. Mammals in montane isolates, western U.S. The abscissa represents log(area); the ordinate represents log (number of species). The data points are taken from (Brown 1971), but are log–log transformed. The solid curve is the log–log graph of $S^*(A)$, where $S^*(A)$ is defined in (1.7). The broken line is the log–log graph of $S(A)=CA^z$; thus C is the y-intercept and z is the slope. The curves were fitted to the data (after a logarithmic transformation) by minimization of the (logarithmic) least squares error $\tilde{E}$ given for $S^*(A)$ in (2.3) and for $S(A)$ in (2.4). The coefficient of determination was computed in terms of the logarithmically transformed data and relations. The computed values of the parameters in $S^*(A)$ and $S(A)$ and of the goodness of fit are as follows: for S^*, $S_0=97$, $\mu=-10.9$, $\sigma=4.91$, (logarithmic) least squares error $\tilde{E}=2.35$, (logarithmic) coefficient of determination $(r^2)=0.671$; for S, $C=0.519$, $z=0.429$, (logarithmic) least squares error $=2.32$, (logarithmic) coefficient of determination $=0.676$. (In (Brown 1971) the quantity r for the relation $S=CA^z$ is computed as 0.82; that agrees with our computation of r^2 to two significant figures.)

The point of our computations is simply to show that in some reasonable sense $S^*(A)$ fits some data sets about as well as $S(A)$. We have plotted the untransformed data and the curves fitted to it for five data sets in Figures 1a–5a. We have plotted the log transformed data and corresponding fitted curves in Figures 1b–5b. The computed values for the parameters in the relations, the least squares errors E or $\tilde{E}$, and the coefficients of determination are given in the figure captions and summarized in Tables I and II. Our conclusion is that $S^*(A)$ gives a slightly better fit to the data than $S(A)$ in some cases but a slightly worse one in others. The overall performance of the two formulations appears to be similar.

We have not made a similar analysis of how well $S^{\#}(A)$ as defined in (1.10) fits the data, since an extensive statistical analysis of $S^{\#}(A)$ versus $S(A)$ (that is, logarithmic versus power law dependence) is given in (Connor and McCoy, 1979) and the comparison has also been discussed in various other articles (for example, (Newmark, 1986)) in specific cases. Some aspects of the analysis in (Connor and McCoy, 1979) are disputed in (Sugihara, 1981). On the basis of published discussion it seems fair to conclude that in many cases $S(A)$ gives a somewhat better fit to the data, but in some cases $S^{\#}(A)$ gives results that are as good or better.

TABLE I

Statistics of Species–Area Models (Untransformed Data)

Type, location, source, and figure showing graphs	Parameters and goodness of fit for S^* S_0	μ	σ	E	r^2	Parameters and goodness of fit for S C	z	E	r^2
Birds, West Indies; Preston 1962, Table IV (Fig. 1a)	140	−5.45	3.18	857	0.93	11.6	0.218	1300	0.894
Birds, East Indies; Preston 1962, Table V (Fig. 2a)	2200	−14.1	4.72	20900	0.895	5.96	0.348	20300	0.897
Land vertebrates, islands in Lake Michigan; Preston 1962, Table VI (Fig. 3a)	1770	−22.4	9.42	531	0.959	9.64	0.238	514	0.961
Land plants, Galapagos; Preston 1962, Table VII (Fig. 4a)	380	−2.63	3.33	73200	0.627	48.8	0.254	77900	0.604
Mammals, montane habitat isolates in the western U.S.; Brown 1971, Table 1 (Fig. 5a)	10.6 (12)	−2.72 (−3.03)	1.46 (1.78)	54.9 (55.6)	0.697 (0.692)	0.793	0.366	64.3	0.644

Note. This table summarizes the information given in the captions of Figs. 1a–5a. The species–area relation defined in (1.7) is denoted by $S^*(A)$; the relation $S(A) = CA^z$ is denoted by $S(A)$. The parameters S_0, μ, and σ are those occurring in (1.7). The quantity E represents the least squares error given for S^* in (2.1) and for S in (2.2). The quantity r^2 is the coefficient of determination. The data were fitted by minimizing E relative to the parameters in $S^*(A)$ and $S(A)$. The values shown in parentheses in the last line of the table are the fitted values of μ and σ and measures of goodness of fit for S^* when S_0 is set equal to 12, which is the largest number of species occurring in the data set. (Since S_0 denotes the size of the total species pool, it should be at least as large as the largest number of species observed in the data set.)

TABLE II

Statistics of Species–Area Models (Log Transformed Data)

Type, location, source, and figure showing graphs	Parameters and goodness of fit for S^* S_0	μ	σ	$\tilde{E}$	r^2	Parameters and goodness of fit for S C	z	$\tilde{E}$	r^2
Birds, West Indies; Preston 1962, Table IV (Fig. 1b)	280	−9.42	5.40	0.211	0.930	9.20	0.244	0.235	0.922
Birds, East Indies; Preston 1962, Table V (Fig. 2b)	2830	−15.5	5.28	0.281	0.908	5.69	0.351	0.274	0.910
Land vertebrates, islands in Lake Michigan; Preston 1962, Table VI (Fig. 3b)	124	−5.00	3.85	0.837	0.922	6.31	0.295	1.30	0.879
Land plants, Galapagos; Preston 1962, Table VII (Fig. 4b)	1600	−11.2	6.42	8.40	0.573	28.6	0.331	8.17	0.585
Mammals, montane habitat isolates in the western U.S.; Brown 1971, Table 1 (Fig. 5b)	97.0	−10.9	4.91	2.35	0.671	0.519	0.429	2.32	0.676

Note. This table summarizes the information given in the captions of Figs. 1b–5b. The species–area relation defined in (1.7) is denoted by $S^*(A)$; the relation $S(A) = CA^z$ is denoted by $S(A)$. The parameters S_0, μ, and σ are those occurring in (1.7). The quantity $\tilde{E}$ represents the (logarithmic) least squares error given for S^* in (2.3) and for S in (2.4). The quantity r^2 is the coefficient of determination. The data were fitted by minimizing $\tilde{E}$ relative to the parameters in $S^*(A)$ and $S(A)$.

IV. Inferences and Speculations on Refuge Design

A major reason for considering mathematical models is that they serve to focus, sharpen, and stimulate discussion. The island biogeography theory of Mac Arthur and Wilson has been used extensively to address questions of refuge design, and has certainly stimulated much discussion; see for example (Diamond, 1975a; Simberloff and Abele, 1976, 1982; Cole, 1981; Newmark, 1986; and references therein). There are two major drawbacks in applying the MacArthur–Wilson theory to refuge design. The first is that in some cases there may not be significant colonization of a refuge, and the MacArthur–Wilson theory assumes a balance between colonization and extinction; this point is raised in (Newmark, 1986). The second is that the MacArthur–Wilson theory does not explicitly incorporate assumptions about community structure. We observed that there has been considerable controversy over the extent to which competition structures communities (see (Diamond, 1975b; Conner and Simberloff, 1979; Gilpin and Diamond, 1982, 1984, 1987; Wilson, 1987). There has also been some controversy about optimal approach to refuge design (see Diamond, 1975a; Simberloff and Abele, 1976, 1982; Connor and McCoy, 1979; Cole, 1981; Blouin and Connor, 1985; Newmark, 1986; Cantrell and Cosner, 1989, 1991a, 1993). Our modeling approach admits a varity of assumptions about community structure with each assumption influencing the conclusions of the theory. The models are based on the assumption that extinction plays a much more significant role than colonization. Hence our models may apply in situations other than those appropriate for the MacArthur–Wilson theory.

If we examine the formulations leading to $S^*(A)$ and $S^{\#}(A)$, there are some immediate and striking differences in the implications for refuge design. Both models suggest that a single large reserve will usually sustain more species than a single small one of similar habitat type. However, the models diverge in their implications for the question of whether it is better to have a single large refuge or several small ones. The assumption leading to $S^*(A)$ is that competitive exclusion is not an important factor in community structure. The implication is that any species which can sustain itself in a reserve with a given area will be represented there. It follows that the faunas of reserves of different sizes should be strictly nested; that is, a larger reserve will contain all those species found in any smaller reserve and perhaps some others. (The nestedness of faunas in certain habitat islands is asserted in (Patterson and Atmar, 1986), for example.) The conclusion is that *if* competitive exclusion plays no major role then a single large reserve should sustain more species than several small ones. On the other hand, the assumption leading to the formulation $S^{\#}(A)$ is that the community structure is strongly influenced by competitive exclusion. If that is the case then two reserves of the same size would be expected to have the same total number of species but might have few or no species in common. Since $S^{\#}(A)$ is concave, it follows that *if* competitive exclusion is a major structuring factor then several small reserves that have different species occupying corresponding niches could very well sustain more species than a single large one in which only one of the possible occupants of each niche would actually be present. Of course, it would be necessary to have several possible species available for many niches for such an effect to occur. Thus, any single small refuge would contain only a fairly low percentage of the species that we might want to preserve. (It is argued in (Cole, 1981) on the basis of a different analytic approach that the situation in which several small refuges would be expected to preserve more species than a single large one is when all the refuges together contain only a small fraction of the overall species pool. Our conclusion is qualitatively similar to Cole's but not as strong.)

The general conclusion of our speculations is that in situations where colonization is not important, if competitive exclusion is not a major factor in structuring a community then one large refuge should preserve more species than several small ones, but if competitive exclusion does structure a community, then several small refuges might be more effective than a single large one. We do not consider these conclusions to be more than speculations, but we do believe that they show how bringing community structure into the models for the species–area relationship allows a more detailed examination of some of the factors affecting the relative merits of different refuge designs. A conclusion suggested by these speculations that we do consider to be important and generally valid is that it is absolutely crucial to understand the detailed ecology of a community or species before trying to decide how best to preserve it. The same sort of conclusion is drawn in Cantrell and Cosner (1991a) on the basis of population dynamics for a single species and in Newmark (1986) on the basis of a number of statistical and empirical arguments.

V. Conclusions and Discussion

Our first and most basic conclusion is that it is possible and worthwhile to formulate a reasonable theory of the insular biogeography of relict populations from standard models of population dynamics with dispersal that are combined with simple hypotheses about community structure. Our models are reasonable from a theoretical viewpoint because they are based on modeling considerations which are widely accepted as plausible in some circumstances. Our models are reasonable from an empirical viewpoint because they are partly based on the observations of (Brown, 1971; Patterson and Atmar, 1986) that extinction may be more important than colonization in structuring some communities, and because they fit some data sets as well as or better than competing models.

A major advantage of our models is that they contain explicit parameters describing the size and shape of the insular habitat and the growth and dispersal rates of the species inhabiting it. In some cases the parameters in the models can be estimated; see (Okubo *et al.*, 1989) as an example. Our assumptions about community structure are either minimal (as in the formulation of $S^*(A)$ in (1.7)) or based on ideas that have proven useful in other theoretical investigations (as in the formulation for $S^{\#}(A)$ in (1.10) on the basis of the sort of niche overlap theory suggested in (Hutchinson, 1959) and developed in (May, 1973).) In any case our models can accommodate various assumptions about population dynamics and community structure, so they can be adapted to different situations and then used for theoretical comparisons. Many other factors such as "advective" transport as in (Murray and Sperb, 1983) or spatial heterogeneity (as in Cantrell and Cosner, 1989, 1991a, 1991b) could also be easily incorporated into the models. Hence, they permit inquiry into how various mechanisms may effect community structure. They do not give a single form for the species–area relation. Instead, they translate assumptions about the distribution of growth and dispersal rates in a community into conclusions about species–area relations. Thus, the modeling approach we have taken permits an explicit analysis and comparison of the implications of different assumptions about a community and its environment. It also allows the derivation of a theory from a mechanistic approach at the population level. We believe that some such approach is needed if we are to better understand the mechanisms leading to the biogeography we observe. The type of models we have described here are relatively elementary; much of their value lies in the fact that they can be expanded, extended, and refined to describe other situations or to include other factors.

We consider our models reasonable from empirical viewpoint because they produce as good a fit to at least some data sets as does the MacArthur–Wilson model, as shown in Tables I and II and the figure captions for $S^*(A)$. We have not performed the analysis for $S^{\#}(A)$, since the modeling leading to the definition of $S^{\#}(A)$ in (1.10) yields a new derivation of the logarithmic or Gleason (1922) form of species–area relation, which in some cases has been shown to fit data well. (See McCoy and Connor, 1979; Newmark, 1986). It is certainly possible to refine the models further, incorporate other effects, and perform more detailed statistical analyses. We intend to pursue some of those ideas in future work and hope that other investigators may do so as well.

The specific models we consider in this paper do not incorporate colonization. That is both a limitation and a strength of those models. The general modeling approach we have taken should be adaptable to some situations where colonization is important, and we intend to pursue that topic further in future work. The models without colonization that we consider here provide a theoretical justification for the application of island biogeographic ideas to situations where colonization is not significant, as discussed in (Brown, 1971; Patterson and Atmar, 1986). In a sense they can be interpreted as explaining why island biogeography theory based on a balance between colonization and extinction gives a good fit to some data sets for which colonization is not a major factor. Since the predictions of our models are numerically similar to those of the MacArthur–Wilson theory in some parameter ranges, they can be viewed as explaining the observation that the MacArthur–Wilson theory gives fairly good results even in situations where the underlying assumptions of a dynamic equilibrium between immigration and extinction may not hold.

We have presented some general reasons why our modeling approach is worth pursuing. There are also certain specific features of the formulation $S^*(A)$ which could be viewed as making it a more attractive description of the species–area relation than the power law. For example, $S^*(A)$ is not linear relative to any standard coordinate transformation. In particular, $S^*(A)$ flattens out to an asymptote as $A \to \infty$. It has been suggested (Schoener, 1976; Martin, 1981) that a good species–area relation should have that feature, and in fact to fit data and predict species numbers in the MacArthur–Wilson theory, Gilpin and Diamond (1976) had to assume conditions on colonization and extinction rates leading to an asymptotic form of species–area curve rather than the more commonly used power law. However, there does not appear to be general agreement on this point; see the discussion in Williamson (1981, pp. 123–126.) In view of the variety and complexity of factors affecting community membership (see Williamson (1981) or Roughgarden (1989)) it seems likely that any specific feature of a model will be an advantage in some situations and a drawback in others. This observation returns us to the point that our models are adaptable to many different situations because they embody explict ecological assumptions that can be tailored to fit a given situation.

A secondary conclusion that can be drawn from the speculations on refuge design is that for effective decision making in refuge design a good understanding of the ecology of the species and/or the community being protected is absolutely essential. The discussion illustrates how similar models which yield reasonable and fairly similar species–area curves can have strongly divergent implications for refuge design. This sort of phenomenon is discussed for single species population models in (Cantrell and Cosner, 1991a) and from a more general ecological viewpoint in (Newmark, 1986). Our speculations in themselves may or may not represent realistic assessments of any actual situations, but they do show

how varying the assumptions about structuring factors can radically change the models' predictions. Of course, such comparisons are possible only in models that incorporate structural assumptions in a fairly explicit way. We hope that our approach can stimulate and focus discussion on which assumptions are appropriate in which sorts of situations.

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