



## Spatial Heterogeneity and Critical Patch Size: Area Effects via Diffusion in Closed Environments

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We describe a class of mathematical models for critical patch size in which the mechanisms inducing area effects are based on source–sink population dynamics arising from dispersal throughout a closed, finite, but spatially heterogeneous environment. Our models are reaction–diffusion equations, but unlike classical KISS models for area effects they do not assume that there is dispersal across the boundary of the environment into a hostile exterior. We observe that simple rescaling has the same effects in our models as in KISS models and hence predicts the same sort of area effects, but that other sorts of rescaling may not predict area effects. The models considered here provide an alternative to the KISS models used in our previous work on species–area relationships in island biogeography.

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### 1. Introduction

Natural systems occupy space and often display variability within the space they occupy. An obvious question is how the size and variability of an environment affects the population or community inhabiting it. In recent years, there has been considerable interest in theoretical approaches to understanding spatial effects in population dynamics; see for example the reviews (Hastings, 1990; Karieva, 1990; Taylor, 1990; Goldwasser *et al.*, 1994; Holmes *et al.*, 1994; Molofsky, 1994; Tilman, 1994). There has also been at least some work on the empirical side as well; there is a review of recent literature on the effects of habitat fragmentation in Doak *et al.* (1992). Both empirical and theoretical aspects of the effects of habitat

geometry and edge permeability on dispersal from habitat patches are discussed in Stamps *et al.* (1987). There has also been considerable recent interest in community level approaches to spatial effects, mostly because of the connections to refuge design, and mostly from the viewpoint of the equilibrium theory of island biogeography of MacArthur & Wilson (1963, 1967). Some of the literature on island biogeography, habitat fragmentation, refuge design, and related issues in conservation is cited in the references of Ehrlich (1989) and Cantrell & Cosner (1989, 1994). Of course, the biogeography of islands has been a focus of theoretical and empirical study since Darwin. Islands lend themselves to studies of spatial effects because they occur in various sizes and at various distances from sources of colonists and have sharply defined boundaries. Many theoretical and empirical issues in island biogeography are discussed in Williamson (1981).

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An examination of the literature shows patterns in the sorts of models typically used to address different aspects of spatial theory. Area effects at the population level are often modeled by reaction–diffusion equations with spatially constant coefficients. Effects related to spatial heterogeneity and dispersal through different habitats are frequently studied via patch models. Area effects at the community level are largely described in terms of species–area curves which are derived from ideas related to the equilibrium theory of island biogeography of MacArthur and Wilson with little or no explicit reference to population dynamics. In many cases, the choice of modeling approach is based on a thoughtful consideration of which sort of model offers the best description of the phenomenon under study, but sometimes the choice is based on the limitations (or perceived limitations) of the mathematics. An example that we shall address in the present article is critical patch size theory and its connections with environmental heterogeneity. The best-known models for critical patch size are called KISS models after Kierstead & Slobodkin (1953) and Skellam (1951). In current usage, a KISS model is generally interpreted as a reaction–diffusion equation for a population density on a bounded region, with the coefficients of the equation being constant on the region and the density going to zero on the boundary of the region. The boundary condition corresponds to a situation where members of the population diffuse randomly across the boundary of the region into an immediately lethal exterior. On the other hand, Skellam (1951) explicitly considered models incorporating spatial heterogeneity via variable coefficients, but commented on such models that “orthodox analytical methods appear to be inadequate . . .” (Skellam, 1951, p. 212). We shall see that mathematical methods developed in the decades since Skellam’s seminal work are now adequate to derive results on critical patch size from reaction–diffusion models incorporating spatial heterogeneity in closed, bounded environments with no dispersal across the boundary. It turns out that the scaling properties of such models are the same as those of standard KISS models. Hence, the derivation of species–area relations from classical KISS models in Cantrell & Cosner (1994) could also be based on the mech-

anism of spatial heterogeneity within islands or other isolated environments rather than dispersal across a boundary into a hostile exterior region. The sort of heterogeneity we envision is variation in the quality of habitat for a single species. The question of how the presence of multiple habitat types affects the number of species present in community is also of interest (see Williamson, 1981) and could be addressed by methods similar to those used here, as in Cantrell & Cosner (1993), but we do not consider that issue.

Since the work of Skellam (1951) and Kierstead and Slobodkin (1953) there have been a number of variations and refinements on their basic models for critical patch size. Ludwig *et al.* (1979) considered situations where there might be multiple equilibria for the population density. Gurney & Nisbet (1975) examined a situation which is closest to those considered here. In their models, the overall environment was considered to be infinite, but the quality of habitat was assumed to be good enough to induce a positive local growth rate on a central region and to become increasingly bad at greater distances from the center. What is different in our present discussion is that we assume the overall environment to be finite with a boundary which is impermeable to the population inhabiting the environment but with arbitrarily arranged interior regions of favorable and unfavorable habitat among which the population may disperse. Thus, we consider dispersal among subregions of a closed environment. The distinction between patches with “hard edges” across which there is no dispersal and those with “soft edges” across which dispersal may occur is studied via simulations in Stamps *et al.* (1987). In the terminology of that paper the situation we consider would be that of a “superpatch” with a hard edge containing one or more soft-edged patches of favorable habitat and also containing soft-edged patches or regions of unfavorable habitat. The sort of natural system we have in mind might be an oceanic island containing a variety of habitat types and inhabited by a population of some terrestrial species. The population dynamics could be viewed as a spatially continuous version of the source–sink dynamics of Pulliam (1988). Our main observation is that spatial rescalings which expand the favorable and unfavorable regions

proportionally without changing their shape or arrangement behave exactly as do rescalings of standard KISS models and hence yield the same results (up to the numerical values of certain constants) on critical patch size. We first make our observations on scaling in Section 2 in the context of simple models, but in Section 3, we describe a reasonably general class of models including density-dependent dispersal for which the scaling results hold. In Section 3, we also discuss alternative sorts of scalings which do not yield a critical patch size, and describe how critical patch size theory based on environmental heterogeneity can be used to obtain species-area relations in island biogeography theory. The species-area relations are obtained from critical patch size theory as in Cantrell & Cosner (1994) but replace the KISS mechanism of dispersal across a patch boundary with something akin to source-sink dynamics within the patch.

There has been some theoretical work on spatial heterogeneity based on reaction-diffusion models with variable coefficients, but other than the work of Gurney & Nisbet (1975), little of it deals explicitly with critical patch size theory or the effects of scaling. Other papers using reaction-diffusion models with spatial variation include Pacala & Roughgarden (1982), Shigesada *et al.* (1986), Cantrell & Cosner (1989, 1991a, b, 1993) and Benson *et al.* (1993). There has been little work on connecting island biogeography theory with population dynamics on the interior of islands; a notable exception is Holt (1992). To our knowledge, the only discussion of island biogeography theory from the viewpoint of reaction-diffusion models is in Cantrell & Cosner (1994).

## 2. Simple Models for Critical Patch Size

### 2.1. REVIEW OF KISS MODELS

The basic form of KISS model for critical patch size, as introduced in Kierstead & Slobodkin (1953) and Skellam (1951) has the form

$$\frac{\partial u}{\partial t} = d \left( \frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2} \right) + ru \text{ in } \Omega, \quad (1)$$

$$u = 0 \text{ on } \partial\Omega, \quad (2)$$

where  $u$  is a population density,  $\Omega$  a finite two-dimensional region, and  $\partial\Omega$  denotes the boundary of  $\Omega$ . The boundary condition (2) is generally interpreted to mean that members of the population diffuse randomly across the boundary of  $\Omega$  and that the exterior of  $\Omega$  is immediately lethal to them. It can be argued in many cases that these assumptions are not realistic. For example, if  $\Omega$  represents an island and the population described by  $u$  consists of terrestrial organisms with an aversion to entering water, we would expect that essentially none of the population would cross  $\partial\Omega$ . A boundary condition describing a situation where no member of the population crosses  $\partial\Omega$  is the Neumann or reflecting boundary condition

$$\frac{\partial u}{\partial n} = 0 \text{ on } \partial\Omega, \quad (3)$$

where  $\partial u / \partial n$  denotes the directional derivative of  $u$  in the direction of the outward pointing normal vector to  $\partial\Omega$ . However, if we consider eqn (1) with boundary condition (3) then the prediction is that any size patch will support growth of the population. We shall see that the situation may be very different if we assume spatial heterogeneity in the growth rate  $r$  in eqn (1).

To understand how the phenomenon of critical patch size can occur for models more general than eqn (1) we shall need to consider certain problems associated with the spatial part of the model and examine how the eigenvalues behave if the region  $\Omega$  is rescaled. We shall follow the approach used in Cantrell & Cosner (1994) for standard KISS models and then show how the method extends to more complicated situations. The first observation is that a population described by eqns (1) and (2) will grow exponentially if the largest eigenvalue  $\sigma_1$  for the problem

$$d \left( \frac{\partial \psi^2}{\partial x^2} + \frac{\partial^2 \psi}{\partial y^2} \right) + r\psi = \sigma\psi \text{ in } \Omega, \quad (4)$$

$$\psi = 0 \text{ on } \partial\Omega$$

is positive, and will decline exponentially if  $\sigma_1$  is negative. In the simple case of eqn (4) the

eigenvalue  $\sigma_1$  can be computed explicitly in terms of the smallest eigenvalue  $\lambda_1$  of the problem

$$\begin{aligned} d\left(\frac{\partial^2\phi}{\partial x^2} + \frac{\partial^2\phi}{\partial y^2}\right) + \lambda r\phi &= 0 \quad \text{in } \Omega, \\ \phi &= 0 \quad \text{on } \partial\Omega. \end{aligned} \tag{5}$$

The connection is that both  $\lambda_1$  and  $\sigma_1$  are uniquely characterized by having positive eigenfunctions, and the eigenfunction  $\phi$  from eqn (5) may be set equal to  $\psi$  in eqn (4) and yields  $\sigma_1 = (1 - \lambda_1)r$ . Thus,  $\sigma_1 > 0$  if  $\lambda_1 < 1$  (predicting population growth) and  $\sigma_1 < 0$  if  $\lambda_1 > 1$  (predicting a decline in population). The second point is that we can understand the relationship between  $\lambda_1$  and the size of  $\Omega$  by considering a region  $\Omega_0$  with the same shape as  $\Omega$  but with unit area and rescaling  $\Omega_0$  to  $\Omega$  by the change of variables  $\tilde{x} = \sqrt{A}x$ ,  $\tilde{y} = \sqrt{A}y$  where  $A$  is the area of  $\Omega$ . If we denote by  $\lambda_0$  the smallest eigenvalue of

$$\begin{aligned} d\left(\frac{\partial^2\phi}{\partial x^2} + \frac{\partial^2\phi}{\partial y^2}\right) + \lambda r\phi &= 0 \quad \text{in } \Omega_0, \\ \phi &= 0 \quad \text{on } \partial\Omega_0 \end{aligned} \tag{6}$$

then we have  $\lambda_1 = \lambda_0/A$ . (We used the same rescaling argument in a slightly different context to obtain Theorem 2 of Cantrell & Cosner (1994) and will discuss the rescaling in more detail in the context of more general models). If we combine the scaling with the condition  $\lambda_1 < 1$  implying population growth we obtain the condition

$$A > \lambda_0 \tag{7}$$

characterizing the critical patch size for population growth in regions having the same shape as  $\Omega_0$ . Finally, we observe that in this simple case we can connect  $\lambda_0$  with the smallest eigenvalue  $\lambda_0^*$  of

$$\begin{aligned} \frac{\partial^2\phi}{\partial x^2} + \frac{\partial^2\phi}{\partial y^2} + \lambda\phi &= 0 \quad \text{on } \Omega_0, \\ \phi &= 0 \quad \text{on } \partial\Omega_0 \end{aligned} \tag{8}$$

by observing that if  $\lambda_0^*$  is an eigenvalue of eqn (8) then  $\lambda_0 = d\lambda_0^*/r$  is an eigenvalue of eqn (6). This leads to the familiar formulation of the critical patch size as

$$A > \lambda_0^* d/r \tag{9}$$

[See e.g. Holmes *et al.*, 1994, eqn (15)].

**Example 1.** In simple geometries it is possible to compute  $\lambda_0^*$  explicitly by using separation of variables to construct the eigenfunction  $\phi$ . If  $\Omega_0$  is a square, of side 1, we obtain  $\phi(x, y) = \sin(\pi x)\sin(\pi y)$ , so that  $\lambda_0^* = 2\pi^2 \approx 19.7$ . If the domain  $\Omega_0$  is rescaled to become a square of area  $A$ , then the eigenvalue  $\lambda_0$  is given by  $\lambda_0 = 2\pi^2/A$  so the condition (9) becomes  $A > 2\pi^2 d/r$ .

## 2.2. DIFFUSION MODELS ON CLOSED REGIONS WITH SPATIAL HETEROGENEITY

The essential assumptions of KISS models are that the population inhabits a homogeneous patch and that the patch boundary of that is completely open to a hostile exterior region in the sense that the population diffuses freely across the boundary. An alternative sort of diffusion model can be based on the assumptions that the patch is spatially heterogeneous and that the population diffuses freely throughout the patch but does not cross the boundary. It can be argued that those assumptions may be more realistic in some cases than those of standard KISS models. Spatial heterogeneity is certainly a feature of many natural systems, and some terrestrial populations might disperse more freely and uniformly between habitats of different quality than they would from an island into the surrounding water; see for example the discussion in Stamps *et al.* (1987). This would especially be likely if the quality of habitat were to vary continuously rather than changing sharply at the edges of subpatches. Population dynamics in a patchy environment with patches of variable quality has been modeled by the source-sink dynamics of Pulliam (1988); however, we are interested in the effects of patch size and variability within a patch, so we consider continuum models with what amount to source-sink dynamics within the

continuum. A simple model embodying the above hypotheses is

$$\frac{\partial u}{\partial t} = d \left( \frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2} \right) + r(x, y)u \quad \text{in } \Omega \quad (10)$$

subject to the boundary condition (3), namely  $\partial u / \partial n = 0$  on the boundary of  $\Omega$ , where  $r(x, y)$  in general is positive on some parts of  $\Omega$  and negative on others. (Recall that the boundary condition describes a perfectly reflecting boundary.) It turns out that the behavior of eqn (10) depends critically on the average quality of the habitat in  $\Omega$  as measured by the integral of  $r(x, y)$  over  $\Omega$ . We can consider the eigenvalue problems for eqn (10) corresponding to eqns (4) and (5). For theoretical reasons we shall consider the analogue of eqn (5) first. The eigenvalue problem corresponding to eqn (5) for eqn (10) is

$$\begin{aligned} d \left( \frac{\partial^2 \phi}{\partial x^2} + \frac{\partial^2 \phi}{\partial y^2} \right) + \lambda r(x, y)\phi &= 0 \quad \text{in } \Omega, \\ \frac{\partial \phi}{\partial n} &= 0 \quad \text{on } \partial\Omega. \end{aligned} \quad (11)$$

This problem will always have a principal eigenvalue which is characterized by having a positive eigenfunction. If  $r(x, y) > 0$ , that principal eigenvalue will be zero and the eigenfunction will be a constant. If  $r(x, y)$  changes sign there may also be a positive principal eigenvalue. The basic result is the following theorem of Brown & Lin (1980):

**Theorem 1.** *Suppose that  $r(x, y)$  is continuous on  $\bar{\Omega}$  and positive on some subregion of  $\Omega$  with positive area. If*

$$\iint_{\Omega} r(x, y) dx dy < 0, \quad (12)$$

*then there is a unique positive principal eigenvalue  $\lambda_1^+(r, \Omega)$  for eqn (11). The principal eigenvalue is characterized by having a positive eigenfunction  $\phi$ .*

**Discussion.** The biological meaning of the hypotheses on the intrinsic local growth rate  $r(x, y)$  is that the growth rate must be positive somewhere in the region  $\Omega$  but must have a negative

average. In other words, there must be some subregion or subregions of  $\Omega$  where the habitat is favorable for the population, but on the average the habitats in  $\Omega$  must be unfavorable. (The average of  $r(x, y)$  is simply the integral appearing in eqn (12) divided by the area of  $\Omega$ .) The presence of relatively large areas of unfavorable habitat in the closed environment corresponding to the boundary condition (3) is the mechanism which replaces diffusion across the boundary of an open environment into a hostile exterior region which corresponds to boundary condition (2). Results, more general than Theorem 1, are obtained in Senn & Hess (1982); see also (Hess, 1991). We shall discuss and apply some of them in the next section. If the boundary condition in eqn (11) is replaced with  $\phi = 0$  on  $\partial\Omega$ , then the theorem will hold without hypothesis (12) (see Manes & Micheletti, 1973; Hess & Kato, 1980).

There are deep connections between the eigenvalue  $\lambda_1^+(r, \Omega)$  occurring in Theorem 1 and the behavior of density-dependent models based partly on eqn (10). We shall describe those in the next section. For our current discussion we need to only consider the connection between  $\lambda_1^+(r, \Omega)$  and the growth or decline of the population described by eqn (10). That connection is made by the eigenvalue problem corresponding to eqn (4):

$$\begin{aligned} d \left( \frac{\partial^2 \psi}{\partial x^2} + \frac{\partial^2 \psi}{\partial y^2} \right) + r(x, y)\psi &= \sigma\psi \quad \text{in } \Omega, \\ \frac{\partial \psi}{\partial n} &= 0 \quad \text{on } \partial\Omega. \end{aligned} \quad (13)$$

As in eqn (4), there is always a unique largest eigenvalue  $\sigma_1$  for eqn (13) and model (10) predicts exponential growth for the population density  $u$  if  $\sigma_1 > 0$  and exponential decay if  $\sigma_1 < 0$ . The connection between  $\sigma_1$ ,  $\lambda_1^+(r, \Omega)$ , and  $r(x, y)$  is given by the following theorem of Senn (1983):

**Theorem 2.** *Suppose that  $r(x, y)$  is continuous in  $\bar{\Omega}$  and is positive at some point  $(x_0, y_0) \in \bar{\Omega}$ .*

(i) *If eqn (12) fails so that*

$$\iint_{\Omega} r(x, y) dx dy \geq 0$$

*then  $\sigma_1 > 0$  in eqn (13).*

(ii) If eqn (12) holds then

$$\sigma_1 > 0 \quad \text{if } \lambda_1^+(r, \Omega) < 1,$$

$$\sigma_1 = 0 \quad \text{if } \lambda_1^+(r, \Omega) = 1,$$

$$\sigma_1 < 0 \quad \text{if } \lambda_1^+(r, \Omega) > 1.$$

**Discussion.** Part (i) can be interpreted as saying that if the habitat quality in  $\Omega$  is high enough to sustain a nonnegative spatially averaged intrinsic local rate of population growth then model (10) always predicts exponential growth. (Recall that we assume  $r$  to be positive somewhere in  $\bar{\Omega}$ .) If the spatially averaged intrinsic local growth rate is negative, as in eqn (12), then eqn (10) predicts growth if  $\lambda_1^+(r, \Omega) < 1$  and decline if  $\lambda_1^+(r, \Omega) > 1$ . This is in exact analogy with the case of KISS models.

The results on which Theorem 2 is based are in Senn (1983, pp. 1204–1205). The notation and sign conventions used are different from those in the present article. In Senn’s notation the quantity corresponding to  $r$  is  $\lambda m$ , and the quantity corresponding to  $\sigma_1$  is  $-\gamma(1)$ . (The meaning of  $\lambda_1$  is the same.)

Since we now have a characterization of the predictions of eqn (10) in terms of  $\lambda_1^+(r, \Omega)$ , we can examine how  $\lambda_1^+(r, \Omega)$  is affected by rescaling.

### 2.3. RESCALING AND CRITICAL PATCH SIZE

To see how eqn (10) subject to condition (12) on  $r(x, y)$  can be interpreted to yield information on critical patch size we examine how the eigenvalue  $\lambda_1^+(r, \Omega)$  behaves under scaling. We use the same scaling here as was used for KISS models in Cantrell & Cosner (1994). Namely, we suppose that  $\Omega_0$  has the same shape as  $\Omega$  but area 1, and that if  $(\tilde{x}, \tilde{y})$  are variables on  $\Omega_0$  we can obtain  $r(x, y)$  by stretching a growth rate  $r_0(\tilde{x}, \tilde{y})$  linearly in each space variable relative to the quadratic increase in area from  $\Omega_0$  to  $\Omega$ . That is, we suppose that  $A$  is the area of  $\Omega$  so that  $(\tilde{x}, \tilde{y}) = (x/\sqrt{A}, y/\sqrt{A})$  and hence  $r(x, y) = r_0(x/\sqrt{A}, y/\sqrt{A}) = r_0(\tilde{x}, \tilde{y})$ . The rescaling is shown graphically in Fig. 1. Note that although the integral of  $r$  over  $\Omega$  is equal to  $A$  times the integral of  $r_0$  over  $\Omega_0$ , the sign of the integral is

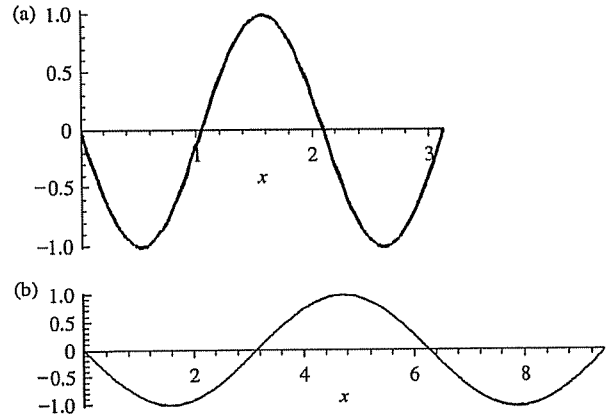


FIG. 1. This figure shows graphs of environmental quality, as measured by the local population growth rate  $r(x)$ , in a pair of one-dimensional environments. The figure shows a rescaling of the environment in which the spatial variable is “stretched” so that the number of regions of favorable habitat ( $r(x) > 0$ ) and unfavorable habitat ( $r(x) < 0$ ) remains the same but the size of each region is increased as the size of the overall environment is increased. The original environment is shown in (a) while the rescaled environment is shown in (b). In this sort of scaling the principal eigenvalue  $\lambda_1^+$  behaves exactly as it would for a KISS model, if the overall spatial environment were expanded by the same factor. In this case, the environment is expanded by a factor of 3 so the eigenvalue would be divided by a factor of 9. (The principal eigenvalue scales as  $(\text{length})^{-2}$  independent of whether the environment is one, two or three dimensional.)

not changed by the scaling and so eqn (12) will hold for  $r$  if it holds for  $r_0$ .

Suppose that  $r_0$  satisfies eqn (12) with respect to  $(\tilde{x}, \tilde{y})$  and  $\Omega_0$ , and let  $\phi_0(\tilde{x}, \tilde{y}) > 0$  be the eigenfunction associated with the principal eigenvalue  $\lambda_1^+(r_0, \Omega_0)$ . We have

$$d \left( \frac{\partial^2 \phi_0}{\partial \tilde{x}^2} + \frac{\partial^2 \phi_0}{\partial \tilde{y}^2} \right) + \lambda_1^+(r_0, \Omega_0) r_0(\tilde{x}, \tilde{y}) \phi_0 = 0$$

in  $\Omega_0$ , (14)

$$\frac{\partial \phi_0}{\partial n} = 0 \quad \text{on } \partial \Omega_0.$$

If we let  $\phi(x, y) = \phi_0(x/\sqrt{A}, y/\sqrt{A}) = \phi_0(\tilde{x}, \tilde{y})$  then, since  $r(x, y) = r_0(x/\sqrt{A}, y/\sqrt{A})$ , we have

$$d \left( \frac{\partial^2 \phi}{\partial x^2} + \frac{\partial^2 \phi}{\partial y^2} \right) = (d/A) \left( \frac{\partial^2 \phi_0}{\partial \tilde{x}^2} + \frac{\partial^2 \phi_0}{\partial \tilde{y}^2} \right)$$

$$\begin{aligned}
 &= -[\lambda_1^+(r_0, \Omega)/A]r_0(\tilde{x}, \tilde{y})\phi_0(\tilde{x}, \tilde{y}) \\
 &= -[\lambda_1^+(r_0, \Omega_0)/A]r(x, y)\phi(x, y)
 \end{aligned} \tag{15}$$

for  $(x, y)$  on  $\Omega$ , with  $\partial\phi/\partial n = (1/\sqrt{A})\partial\phi_0/\partial n = 0$  for  $(x, y)$  on  $\partial\Omega$ . By eqn (15), we have  $\phi > 0$  satisfying

$$d\left(\frac{\partial^2\phi}{\partial x^2} + \frac{\partial^2\phi}{\partial y^2}\right) + [\lambda_1^+(r_0, \Omega_0)/A]r(x, y)\phi \quad \text{in } \Omega, \tag{16}$$

$$\frac{\partial\phi}{\partial n} = 0 \quad \text{on } \partial\Omega,$$

so by the uniqueness of the principal eigenvalue in eqn (11) we have  $\lambda_1^+(r, \Omega) = \lambda_1^+(r_0, \Omega_0)/A$ . Hence, by Theorem 2, the criterion  $\sigma_1 > 0$  for population growth in eqn (10) is equivalent to  $\lambda_1^+(r, \Omega) < 1$ , which is equivalent to

$$A > \lambda_1^+(r_0, \Omega_0). \tag{17}$$

This is identical to the characterization (7) for KISS models. If we let  $\lambda_1^*(r_0, \Omega_0)$  be the principal eigenvalue for

$$\begin{aligned}
 \frac{\partial^2\phi}{\partial \tilde{x}^2} + \frac{\partial^2\phi}{\partial \tilde{y}^2} + \lambda r_0(\tilde{x}, \tilde{y})\phi &= 0 \quad \text{on } \Omega_0, \\
 \frac{\partial\phi}{\partial n} &= 0 \quad \text{on } \partial\Omega_0,
 \end{aligned} \tag{18}$$

we would have  $\lambda_1^* = \lambda_1^+(r_0, \Omega_0)/d$  so that we could rewrite eqn (17) as

$$A > d\lambda_1^*(r_0, \Omega_0) \tag{19}$$

in analogy to eqn (9). If we attach a parameter to  $r(x, y)$  so that  $r(x, y) = \rho r^*(x, y) = \rho r_0^*(\tilde{x}, \tilde{y})$  then eqn (19) becomes

$$A > (d/\rho)\lambda_1^*(r_0^*, \Omega_0). \tag{20}$$

The reason for attaching such a parameter would be for purposes of comparison between species with similar habitat needs (as measured by  $r_0^*$ )

but which reproduce and/or disperse at different rates (as measured by  $\rho$  and  $d$ , respectively). For example, a species whose members allocate a high percentage of consumed resources to physiological reserves might have a slow reproductive rate in favorable habitats but a slow starvation rate in unfavorable habitats, which would be reflected by a small value for  $\rho$ . A species whose members allocate resources primarily to reproduction might increase in numbers rapidly in favorable habitats but starve quickly in unfavorable habitats, which would be reflected by a large value for  $\rho$ .

**Example 2.** Suppose that  $\Omega_0$  is a square with side 1, that  $d = 1$ , and  $r_0(x, y)$  depends only on  $x$ , so  $r_0(x, y) = r_0(x)$ . If  $r_0(x)$  is given by

$$r_0(x) = \begin{cases} -1, & 0 < x < 0.3 \\ 1, & 0.3 < x < 0.7, \\ -1, & 0.7 < x < 1, \end{cases}$$

then eqn (12) holds and  $\lambda^+(r_0, \Omega_0) > 0$ . In this case  $\lambda^+(r_0, \Omega_0)$  can be calculated via the methods of Cantrell & Cosner (1991a). (Essentially the idea is to construct the eigenfunction  $\phi = \phi(x)$  by solving explicitly on each subinterval where  $r_0(x)$  is constant, keeping the eigenvalue to be determined as a parameter, and matching  $\phi(x)$  and  $d\phi/dx$  across the discontinuities of  $r_0(x)$ .) This calculation yields  $\lambda_1^+(r_0, \Omega_0) \approx 10.2$ . If  $\Omega$  is a square with area  $A$  and  $r(x, y) = r_0(x/\sqrt{A})$  then  $\lambda_1^+(r, \Omega) = \lambda_1^+(r_0, \Omega_0)/A \approx 10.2/A$ .

### 3. Connections and Variations

#### 3.1. A DIFFERENT SORT OF SPATIAL RESCALING

The sort of spatial rescaling discussed in the previous section and illustrated in Fig. 1 is only one way in which a larger region could be related to a smaller one. Under that sort of rescaling, the arrangement of favorable and unfavorable habitats does not change but the size of both does. For example, if in  $\Omega_0$  there is a single region with  $r_0 > 0$  then in  $\Omega$  there will still be only a single region with  $r > 0$  but the size of that region will change, as shown in Fig. 1. Another possible way in which a larger region might be related to a smaller region would be if the larger region

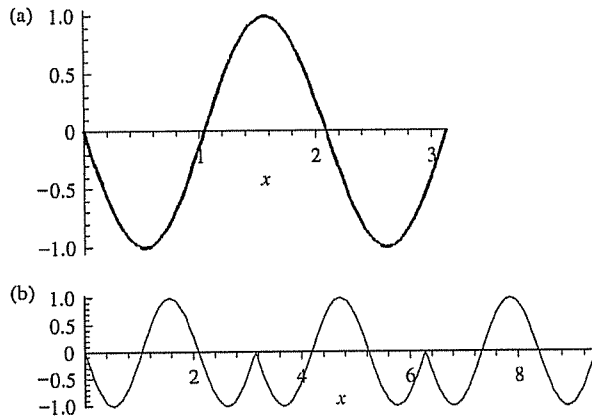


FIG. 2. This figure again shows graphs of environmental quality, as measured by the local population growth rate  $r(x)$ , in another pair of one-dimensional environments, but with a different sort of scaling. The original environment, as shown in (a) is the same as in Fig. 1(a). (b) Shows a rescaling of the environment in which the spatial variable is not “stretched” but where the larger environment consists of a number of copies of the smaller environment which have been joined together. In this scaling, the number of regions of favorable habitat ( $r(x) > 0$ ) and unfavorable habitat ( $r(x) < 0$ ) is increased as the size of the overall environment is increased, while the size of each favorable or unfavorable region remains the same. This sort of scaling leaves the principal eigenvalue  $\lambda_1^+$  unchanged. The reason why increasing the total amount of favorable habitat does not change  $\lambda_1^+$  and thus does not affect predictions of persistence or extinction for the population is that in this case the scaling also increases the number of internal interfaces with regions of unfavorable habitat, which in turn increases the likelihood that individuals will disperse into unfavorable regions. [See Cantrell and Cosner (1989, 1991a, b) for further discussion of this point and related topics.]

consisted, in effect, of several connected copies of the smaller region. This is illustrated in Fig. 2.

This sort of rescaling will typically have little or no effect on  $\lambda_1^+$  and thus does not lead to a simple rescaling relation as in eqns (7), (9), (17), (19) and (20), since it may well be the case that  $\lambda_0(r_0, \Omega_0) = \lambda_1^+(r, \Omega)$ . To see this, suppose that  $\Omega_0$  is a square and that  $r_0$  is symmetric with respect to the center of the square. The eigenfunction  $\phi_0(x, y)$  will then also be symmetric with respect to the center of the square, and will have normal derivative  $\partial\phi_0/\partial n = 0$  on the boundary of the square. To obtain an eigenfunction  $\phi$  on  $\Omega$  we could simply take  $\phi$  to be a translated copy of  $\phi_0$  on each of the translated copies of  $\Omega_0$  making up  $\Omega$ . (Since  $\phi_0$  was symmetric and had  $\partial\phi_0/\partial n = 0$  on the boundary of  $\Omega_0$ , the copies would

fit together to form a smooth function  $\phi$  on all of  $\Omega$ .) At any point of  $\Omega$ , the eigenfunction  $\phi$  would satisfy a spatially translated copy of eqn (14), so in that case we would have  $\lambda_1^+(r_0, \Omega_0) = \lambda_1^+(r, \Omega)$ . The difference between the sort of rescalings illustrated in Figs 1 and 2 is that although the total amount of favorable habitat is increased in both rescalings, in Fig. 2 the number of internal transitions between favorable and unfavorable habitats is also increased, so the probability of an individual dispersing into an unfavorable region is not decreased from what it would be on the original smaller region  $\Omega_0$ . A related effect can be observed if the area of  $\Omega$  and the integral of  $r(x, y)$  (i.e. the average quality of the habitat) or the total size and degree of favorability of the favorable and unfavorable regions are kept fixed, but  $r(x, y)$  becomes more oscillatory. For example, this would occur if  $\Omega$  were the unit square and we took  $r_n(x, y) = \sin(2\pi nx) \sin(2\pi ny) - 1/2$ . As  $n \rightarrow \infty$ ,  $r_n(x, y)$  becomes highly oscillatory. Basically, this would reflect a fragmentation of the favorable regions within  $\Omega$ . By the methods of Cantrell & Cosner (1989, 1991a, b) it can be seen that  $\lambda_1^+(r_n(x, y), \Omega) \rightarrow \infty$  as  $n \rightarrow \infty$ , so that a sufficient amount of habitat fragmentation would yield  $\lambda_1^+ > 1$  and hence predict extinction for the population in question. Again, the mechanism causing the detrimental effect would be the increased likelihood of an individual dispersing in such a way that it experienced its habitat on the average as being unfavorable.

**Example 3.** Suppose that  $\Omega_0$  is again a square with side 1, and  $r_0(x, y) = r_0(x)$  is as in Example 2:

$$r_0(x) = \begin{cases} -1, & 0 < x < 0.3, \\ 1, & 0.3 < x < 0.7, \\ -1, & 0.7 < x < 1. \end{cases}$$

If we take  $\Omega$  to be a larger square made from 4, 9, and 25, or in general  $n^2$  copies of  $\Omega_0$  put together to form a square, then by the symmetry of  $r_0(x)$  and hence of  $\phi(x)$ , the eigenfunction for the larger region will consist of copies of  $\phi(x)$  (in the same way that  $r(x)$  will consist of copies of  $r_0(x)$ , repeated in the way shown in Fig. 2). Because the original forms of  $r_0(x)$  and  $\phi(x)$  are not stretched, merely repeated, they satisfy the original



eigenvalue equation with the value of  $\lambda$  unchanged. Hence, we have  $\lambda_1^+(r, \Omega) = \lambda_1^+(r_0, \Omega_0) \approx 10.2$ , as long as  $\Omega$  consists of  $n^2$  copies of  $\Omega_0$  and  $r$  consists of  $n^2$  copies of  $r_0$ , for any integer  $n$ .

### 3.2. INSULAR BIOGEOGRAPHY

In Cantrell & Cosner (1994) a theory of species–area relationships in insular biogeography was developed from KISS models via eqn (9). The goal of that paper was to construct an alternative to the well-known equilibrium theory of island biogeography of MacArthur & Wilson (1963, 1967) on the basis of spatially explicit models for population dynamics. The key idea was to hypothesize a distribution  $s(p)$  of values of the ratio  $r/d$  across a community, so that the number of species with  $a < r/d < b$  would be given by the integral of  $s(p)$  from  $a$  to  $b$ . Rewriting eqn (9) as  $r/d > \lambda_0^*/A$  and hypothesizing that any species whose area requirements are met will be present in the community which would then yield the species–area relation

$$S(A) = \int_{\lambda_0^*/A}^{\infty} s(p) dp. \quad (21)$$

In Cantrell & Cosner (1994) we considered in detail the case where  $s(p)$  was lognormal, but there are many other reasonable choices. A possible criticism of the approach is that it was based on KISS models, which are considered by some to be quite unrealistic in their treatment of the behavior of individuals at the boundary of an island. However, if we replace  $r$  by  $\rho$  and  $\lambda_1^*$  by  $\lambda_1^*(r_0^*, \Omega_0)$  and use eqn (20) instead of eqn (9) we get exactly the same species–area relation shown in eqn (21). The only difference is that the mechanism producing the area effect is spatial heterogeneity rather than dispersal across a boundary into a hostile exterior region. The possible relevance of spatial heterogeneity in terms of multiple habitat types is discussed in Williamson (1981, p. 118–125). To give a full treatment of the effects of multiple habitat types for multiple species, it would require an examination of a set of models where  $r_0(x, y)$  was qualitatively different for different ensembles of species. We shall not pursue that point further at the present time, except to point out that it certainly would be

possible to apply the present methods in such a context (see e.g. Cantrell & Cosner, 1993).

### 3.3. MORE GENERAL MODELS

It can be argued that many sorts of organisms have density-dependent rates of population growth and disperse in more complex ways than via simple diffusion. Two likely variations on diffusion are dispersal to avoid crowding and directional dispersal in the direction of more favorable habitats. If we wish to describe a population with a logistic rate of growth, a density-dependent rate of random dispersal that increases with crowding, and which disperses in a directed way along gradients of increasing habitat quality, the basic models (1) and (3) should be replaced by

$$\begin{aligned} \frac{\partial u}{\partial t} = & \frac{\partial}{\partial x} \left( d(u) \frac{\partial u}{\partial x} \right) + \frac{\partial}{\partial y} \left( d(u) \frac{\partial u}{\partial y} \right) \\ & - \alpha \left[ \frac{\partial}{\partial x} \left( \frac{\partial r}{\partial x} u \right) + \frac{\partial}{\partial y} \left( \frac{\partial r}{\partial y} u \right) \right] \quad (22) \\ & + r(x, y)u - c(x, y)u^2 \quad \text{in } \Omega \end{aligned}$$

with  $u$  satisfying a boundary condition corresponding to eqn (3) on  $\partial\Omega$  for all  $t > 0$ . In eqn (22) we would assume that  $d(u)$  is increasing with  $u$ , with  $d(0) > 0$ , that  $\alpha$  is a nonnegative constant describing the strength of the tendency of the population to move up the gradient of  $r(x, y)$ , and  $c(x, y)$  is a positive function which describes logistic self-limitation. Models of the general type shown in eqn (22) were studied in Cantrell & Cosner (1991b) under the boundary condition (2). If eqn (12) is satisfied then results corresponding to those of Cantrell & Cosner (1991b) will hold for eqn (22) under the reflecting boundary condition shown in eqn (23). The first relevant point is that under hypothesis (12) the associated linear eigenvalue problem given by

$$\begin{aligned} d(0) \left( \frac{\partial^2 \phi}{\partial x^2} + \frac{\partial^2 \phi}{\partial y^2} \right) - \alpha \left[ \frac{\partial}{\partial x} \left( \frac{\partial r}{\partial x} \phi \right) + \frac{\partial}{\partial y} \left( \frac{\partial r}{\partial y} \phi \right) \right] \\ + \lambda r \phi = 0 \quad \text{in } \Omega, \quad (23) \end{aligned}$$

$$d(0) \frac{\partial \phi}{\partial n} - \alpha \frac{\partial r}{\partial n} \phi = 0 \quad \text{on } \partial\Omega$$

has a positive principal eigenvalue  $\lambda_1^+(\alpha, r, \Omega)$  provided  $\partial r/\partial n \leq 0$  on  $\partial\Omega$ . This follows from results of Senn & Hess (1982) and Senn (1983); related results are discussed in some detail in Belgacem (1994). The second key point is that model (22) with boundary condition (3) predicts persistence for the population exactly when  $\lambda_1^+(\alpha, r, \Omega) < 1$ . This follows from the methods used to treat the corresponding problem under boundary condition (2) in Cantrell & Cosner (1991b) with no major changes in the analysis; see also Senn (1983) for related work on models with purely linear diffusion. The final observation is that because of the structure of eqn (23) the eigenvalue  $\lambda_1^+(\alpha, r, \Omega)$  has the same scaling properties as do the principal eigenvalues in eqns (13) and (14), so that  $\lambda_1^+(\alpha, r, \Omega) = \lambda_1^+(\alpha, r_0, \Omega_0)/A$ . The scaling properties are the same because the term describing directed motion along environmental gradients still involves taking two derivatives with respect to the spatial variables. Thus, the discussion of scaling in the case of the simpler model (10) extends to more general models of the form (22).

#### 3.4. COMPUTABLE ESTIMATES AND EIGENVALUE DEPENDENCE ON $r(x, y)$

It is natural to ask whether  $\lambda_1^+(r, \Omega)$  can be computed explicitly. In general, the answer is no. However, the condition that  $r(x, y)$  be continuous in the simple models of Section 2 can be weakened to allow piecewise continuous growth rates. In the case of models in a single space dimension, eigenvalues corresponding to cases where  $r = r(x)$  is a step function, were characterized in terms of equations involving trigonometric and hyperbolic functions in Cantrell & Cosner (1991a). Those characterizations could be used for numerical computation; they were exploited in Cantrell & Cosner (1991a) to study the qualitative dependence of  $\lambda_1^+(r, \Omega)$  on the spatial arrangement of positive and negative values of  $r$ . (Recall that positive and negative values of  $r$  correspond to regions of favorable and unfavorable habitat, respectively.)

#### 4. Conclusions

Our basic conclusion is that the prediction of KISS models of a critical patch size needed to

sustain a population can also be obtained from a reasonably broad range of reaction–diffusion models in which the mechanism producing the critical patch size is spatial heterogeneity within the patch rather than dispersal across the patch boundary into a hostile exterior region as in classical KISS models. More precisely, the mechanism inducing a critical patch size in our models is the interaction of a continuum version of source–sink dynamics (Pulliam, 1988) within a closed patch with spatial scaling of the source and sink regions. To produce the effect, the scaling must increase the size of subregions of favorable (and unfavorable) habitat as the size of the patch increases. Scalings in which the number of favorable subregions increases with patch size but the size of those subregions does not increase will not produce the critical patch size phenomenon.

A secondary conclusion is that the derivation of a species–area curve in insular biogeography theory from KISS models in Cantrell & Cosner (1994) could also be based on spatial heterogeneity via the models presented here. In the case of insular habitats with sharp boundaries such as true islands, the hypothesis of closed patch with internal variation might be more realistic than that of an open patch with dispersal across the boundary. The ideas discussed here and in Cantrell & Cosner (1994) are related to those discussed in Holt (1992) in that the internal population dynamics of the island are considered as an aspect of the theoretical approach to biogeography.

Our final conclusion is more general and philosophical. We believe that the ideas presented in this article suggest that the division of spatial models into KISS models for area effects, patch models for spatial heterogeneity, and stochastic models for colonization and extinction and hence for island biogeography is somewhat artificial from the modeling viewpoint. There are sound ecological reasons for preferring certain types of models for certain situations, but the choice need not be based on the supposed mathematical limitations of some theoretical approach. Much more can be built into or extracted from mathematical models than what has appeared in the ecological literature to date.

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