

## THE IMPLICATIONS OF MODEL FORMULATION WHEN TRANSITIONING FROM SPATIAL TO LANDSCAPE ECOLOGY

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**ABSTRACT.** In this article we compare and contrast the predictions of some spatially explicit and implicit models in the context of a thought problem at the interface of spatial and landscape ecology. The situation we envision is a one-dimensional spatial universe of infinite extent in which there are two disjoint focal patches of a habitat type that is favorable to some specified species. We assume that neither patch is large enough by itself to sustain the species in question indefinitely, but that a single patch of size equal to the combined sizes of the two focal patches provides enough contiguous favorable habitat to sustain the given species indefinitely. When the two patches are separated by a patch of unfavorable matrix habitat, the natural expectation is that the species should persist indefinitely if the two patches are close enough to each other but should go extinct over time when the patches are far enough apart. Our focus here is to examine how different mathematical regimes may be employed to model this situation, with an eye toward exploring the trade-off between the mathematical tractability of the model on one hand and the suitability of its predictions on the other. In particular, we are interested in seeing how precisely the predictions of mathematically rich spatially explicit regimes (reaction-diffusion models, integro-difference models) can be matched by those of ostensibly mathematically simpler spatially implicit patch approximations (discrete-diffusion models, average dispersal success matrix models).

### 1. Introduction.

1.1. **Problem overview.** Habitat fragmentation is a major issue in spatial and landscape ecology as well as a major concern from the viewpoint of conservation. Patch models provide a useful theoretical framework in which ecologists can abstract various aspects of the process of habitat fragmentation. In particular, two-patch models are widely employed for this purpose. There are two main types of patch

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models: patch occupancy models, such as metapopulation models, and spatially distributed population dynamical models, such as discrete diffusion models. Patch occupancy models typically track the time evolution of either the likelihood that a focal species or collection of species occupies any given patch or the fraction of patches so occupied. More often than not, the number of patches under consideration is large, corresponding to an underlying assumption that if a species maintains its presence in an archipelago of patches, it does so by a dynamic process of local extinctions and re-colonizations. Usually individual patches are not viewed as being permanently occupied. However, it is entirely possible to contemplate two-patch environments from the perspective of patch occupancy models.

On the other hand, spatially distributed population dynamical patch models are quite frequently employed in a two-patch context. As with patch occupancy models, space is represented abstractly and implicitly. In this case, a network of discrete sites and the pathways among them are envisioned. The numerical quantities of interest are the average densities of one or more focal species in the collection of sites, and such models track the temporal evolution of these average densities. Spatially distributed population dynamical patch models are often used as “cut-down” surrogates for models in which space is explicitly represented, such as reaction-diffusion models. In so doing, a significant trade-off is made. Such patch models are usually far more tractable analytically and numerically than their spatially explicit counterparts. However, this feature comes at a cost. Namely, in order to consider only average densities in patches, spatial variation in the environment and in the densities themselves must be aggregated to the possible detriment of precision and nuance.

The purpose of this article is to consider the impact of this trade-off in the context of a thought problem at the intersection of spatial and landscape ecology. We envision a one-dimensional spatial universe of unlimited extent in which there are two disjoint focal patches of a habitat type that is favorable to some specified species. Neither patch by itself is large enough to sustain the species in question indefinitely, but a single patch of a size equal to the combined sizes of the two focal patches would be sufficient to sustain a population of the given species indefinitely. Under these circumstances, it is certainly plausible to expect that if the distance between the two patches is small enough, the species could persist indefinitely in the larger landscape. On the other hand, if the favorable patches are too far apart, the connection between them becomes tenuous as far as the focal species is concerned, and one would not expect the species to persist in the larger landscape.

We aim to compare the conclusions that may be drawn about this thought problem from the perspective of spatially explicit models with those that may be drawn from their spatially distributed population dynamical patch model approximations. In this regard, we consider two regimes. In Section 2, we examine the problem via reaction-diffusion models and discrete-diffusion patch model approximations thereof. We first formulate the relevant model in the reaction-diffusion context and describe its predictions. Our goal in this section is to see how closely we can replicate these predictions via those of the more mathematically tractable discrete-diffusion patch models. The mathematical underpinnings of the reaction-diffusion approach are well understood (see, for example, Cantrell and Cosner [3]). Nevertheless, the details of the model analysis required in this specific context are rather intricate, and, we believe, of some independent interest. However, it is not necessary to present them fully in order to compare the predictions from the reaction-diffusion

models to the predictions of the discrete-diffusion patch model approximations. Consequently, since our focus is on seeing how closely we can match predictions of spatially explicit models using mathematically simpler patch models, we will reserve a complete analysis of the reaction-diffusion models for another venue, presenting full details of model analysis only for the discrete-diffusion patch models. In Section 3, we carry out a companion program in the context of spatially explicit integrodifference models with exponential kernels [12] and their average dispersal success patch model approximations [5]. Again our focus is on how closely the predictions of the approximate models match those of the spatially explicit models. As in Section 2, the mathematical analysis of the spatially explicit models under consideration in Section 3 is involved, but nevertheless builds upon established results ([12],[2]). Consequently, as in Section 2, we defer the complete analysis to another venue and concentrate here on the details of the analysis of the patch model approximations. In Section 4, we will summarize and discuss our findings. Our primary focus is on seeing how well the predictions of spatially distributed patch models regarding the thought problem at hand match those of their spatially explicit counterparts. However, as we have noted, it is entirely possible to consider the question from the perspective of patch occupancy models. Indeed, it is relatively easy to carry out the relevant analysis, and moreover, the predictions from the patch occupancy framework serve to enhance our discussion. Consequently, before turning our attention to reaction-diffusion models and their discrete-diffusion approximations, we briefly consider the thought problem via metapopulation theory.

## 1.2. Metapopulation formulation.

1.2.1. *Model formulation and analysis.* In its most basic form [9], (due to Levins in 1969) metapopulation theory describes a species which inhabits an environment consisting of discrete sites, and which may colonize empty sites or experience local extirpations in occupied sites. Suppose now that  $p$  represents the fraction of sites under consideration which are occupied by the species in question at time  $t$ , so that  $0 \leq p(t) \leq 1$ . Let  $c$  be the rate at which colonists are produced if all sites are occupied, so if a fraction  $p$  of sites are occupied then the rate at which colonists are produced is  $cp$ . All sites are assumed to be equally accessible to colonists, so the fraction of sites which are unoccupied when colonists reach them is  $1 - p$ . Then the total rate of colonization of empty sites is  $cp(1 - p)$ . Let  $e$  be the rate of local extinctions on occupied sites. Then the continuous time Levins model for the evolution of the fraction of sites occupied is

$$\frac{dp}{dt} = (c - e)p - cp^2 \quad (1)$$

Equation (1) is simply the well-known logistic equation, so that a positive fraction of approximately  $\frac{c - e}{c}$  may be expected to be occupied long term whenever  $c > e$ .

The Levins model (1) ignores aspects of the population structure [11], in particular the size and geographic arrangement of the patches of habitat in question. These features are incorporated into refinements of the Levins model (1), due to Hanski and his collaborators (see, for example, [6], [7], [8], and [11] for discussion

and references), and are of the form

$$\frac{dp_i}{dt} = \left( \sum_{\substack{j=1 \\ j \neq i}}^n C e^{-\alpha d_{ij}} A_j p_j \right) (1 - p_i) - \left( \frac{E}{A_i} \right) p_i. \quad (2)$$

In (2), the archipelago of habitats consists of  $n$  patches, with patch  $i$  having area  $A_i$  and  $d_{ij}$  designating the nearest distance between patch  $i$  and patch  $j$ . The state variable  $p_i$  now represents the probability that patch  $i$  is occupied by the species in question, while  $C$ ,  $\alpha$ , and  $E$  are positive constants describing the propensity of the species in question to send out colonists, to die during transit through the matrix between patches, and to experience local extinctions, respectively.

Let us now examine the special case of two patches in a one-dimensional world. In this case, (2) reduces to

$$\begin{aligned} \frac{dp_1}{dt} &= C e^{-\alpha D} \ell p_2 (1 - p_1) - \frac{E}{L} p_1 \\ \frac{dp_2}{dt} &= C e^{-\alpha D} L p_1 (1 - p_2) - \frac{E}{\ell} p_2, \end{aligned} \quad (3)$$

where  $D = d_{12} = d_{21}$  is the distance between the two patches,  $A_1 = L$  is the length of patch 1, and  $A_2 = \ell$  is the length of patch 2. Without loss of generality, we adopt the convention that  $\ell \leq L$ . As  $p_1$  and  $p_2$  are interpreted as probabilities, (3) is only meaningful on the set of values  $(p_1, p_2) : 0 \leq p_i \leq 1, i = 1, 2$ . It is evident from the structure of (3) that the system is invariant on this set. Moreover, it follows as in [3] that (3) predicts that the probability that the species in question is present on both patches is positive long term precisely when the linearization of the right hand side of (3) about  $\begin{pmatrix} 0 \\ 0 \end{pmatrix}$  has a positive eigenvalue which admits a componentwise positive eigenvector. Otherwise, the species is expected to go extinct on both patches. Now the linearization of the right hand side of (3) about  $\begin{pmatrix} 0 \\ 0 \end{pmatrix}$  is

$$\begin{pmatrix} -\frac{E}{L} & C e^{-\alpha D} \ell \\ C e^{-\alpha D} L & -\frac{E}{\ell} \end{pmatrix}. \quad (4)$$

Since the off-diagonal terms in (4) are both positive, it follows from the theory of nonnegative matrices [1] that both eigenvalues of (4) are real-valued and that the larger of the two eigenvalues admits a componentwise positive eigenvector. It is easy to calculate that the eigenvalues of (4) are

$$1/2 \left( -\frac{E(L + \ell)}{L\ell} \pm \sqrt{\left( \frac{E(L - \ell)}{L\ell} \right)^2 + 4C^2 e^{-2\alpha D} L\ell} \right)$$

and that (4) has a positive eigenvalue precisely when

$$C^2 e^{-2\alpha D} L\ell > \frac{E^2}{L\ell}. \quad (5)$$

Note that (5) requires that

$$L\ell > \frac{E}{C} \quad (6)$$

and that

$$D < (1/\alpha) \ln\left(\frac{CL\ell}{E}\right). \quad (7)$$

1.2.2. *Model predictions.* Since

$$L + \ell \geq 2\sqrt{L\ell}, \quad (8)$$

(6) imposes the requirement

$$L + \ell > 2\sqrt{\frac{E}{C}} \quad (9)$$

on the minimum combined size of habitat fragments relative to the colonization and extinction rates that is necessary for a prediction of persistence of the species in the two patch archipelago. In turn, (7) may be viewed as a limit on how far apart the fragments may be, given that (6) holds.

Notice that (9) is not equivalent to (6), since equality obtains in (8) only when  $L = \ell$ . This fact has significant ramifications for the model. To this end, suppose we fix an overall favorable habitat of size  $M > 2\sqrt{\frac{E}{C}}$ , let  $\ell \in [0, M/2]$ , and set  $L = M - \ell$ . Then for any  $\ell \in [0, M/2]$ , (9) holds. If  $L = \ell = M/2$ ,  $L\ell = M^2/4 > (1/4)(\frac{4E}{C}) = \frac{E}{C}$  and thus (6) holds. However, since  $\lim_{\ell \rightarrow 0} \ell(M - \ell) = 0$ ,  $L\ell \leq \frac{E}{C}$  for  $\ell$  small enough relative to  $L$ . In such cases, (6) fails and the model predicts extinction for the species in question, no matter how close the two habitat fragments of length  $L$  and  $\ell$  are to each other. This feature is a consequence of the assumption in the model that the extinction rate in a habitat patch is inversely proportional to the size of the patch. Thus if the smaller habitat patch is too small relative to the size of the larger patch, the Hanski refinement of metapopulation theory predicts extinction in the two-patch system even when the combined size of the two patches is large enough to sustain the metapopulation in the case of patches of equal size that are sufficiently close to each other.

## 2. Reaction-diffusion versus discrete-diffusion formulation.

### 2.1. Reaction-diffusion formulation.

2.1.1. *The model.* Here the state variable  $u$  at hand represents the density of a species along a one-dimensional axis of infinite extent. This axis contains two disjoint finite intervals (i.e. patches) consisting of habitat favorable to the species, adjacent to “matrix” habitat which is unfavorable to the species. In particular, the two favorable patches are separated by a patch of unfavorable habitat. The lengths of the favorable patches are  $L$  and  $\ell$ , respectively, where without loss of generality we assume  $\ell \leq L$ , while the length of the patch of unfavorable habitat in between the two favorable patches is  $D$ . The quality of the environment is reflected here via the local growth rate of the species. We assume the local growth rate is a positive constant  $r^2$  in the two favorable patches, and is normalized to  $-1$  in the unfavorable regions. Since the local growth rate is a negative constant asymptotically along the one-dimensional axis, it is reasonable to expect that the density should tend to 0 asymptotically along the one-dimensional axis. We assume that the dispersal is basic Fickian diffusion with constant rate  $d > 0$ .

A linear reaction-diffusion model for  $u = u(x, t)$  which captures the preceding scenario is :

$$u_t = du_{xx} + m(x)u \quad (10)$$

on  $\mathbb{R} \times (0, \infty)$

$$u(x, t) \rightarrow 0 \quad (11)$$

as  $x \rightarrow \pm\infty, t > 0$ . The local growth rate  $m(x)$  in (10)-(11) is given by

$$m(x) = \begin{cases} -1 & x < 0 \\ r^2 & 0 < x < L \\ -1 & L < x < L + D \\ r^2 & L + D < x < L + D + \ell \\ -1 & x > L + D + \ell. \end{cases} \quad (12)$$

Here we have placed the larger favorable habitat patch to the left of the smaller favorable habitat patch, with the left end of the larger patch fixed at the origin. Clearly, there is no loss of generality in these choices.

*2.1.2. Principal eigenvalues.* The prediction of (10)-(11) is determined via the associated eigenvalue problem [4]

$$dv_{xx} + m(x)v = \sigma v \quad (13)$$

in  $\mathbb{R}$

$$v \rightarrow 0 \quad (14)$$

as  $x \rightarrow \pm\infty$

$$v > 0 \quad (15)$$

in  $\mathbb{R}$ . Namely, when the eigenvalue  $\sigma$  in (13)-(15) is positive, (10)-(11) predicts growth of the density  $u$ , whereas, when  $\sigma$  in (13)-(15) is negative, (10)-(11) predicts  $u$  decays toward extinction. The sign of  $\sigma$  in the eigenvalue problem (13)-(15) is directly related to the value of the parameter  $\lambda$  in the weighted eigenvalue problem

$$w_{xx} + \lambda m(x)w = 0 \quad (16)$$

in  $\mathbb{R}$

$$w \rightarrow 0 \quad (17)$$

as  $x \rightarrow \pm\infty$

$$w > 0 \quad (18)$$

in  $\mathbb{R}$ . Here  $\lambda$  corresponds to  $1/d$ . The assumption that  $m(x) = -1$  outside the interval  $[0, L + D + \ell]$  guarantees the existence of a unique necessarily positive eigenvalue  $\lambda_1$  to (16)-(18) [2]. Having the observed value of  $\lambda = 1/d$  exceed  $\lambda_1$  in (16)-(18) corresponds to  $\sigma > 0$  in (13)-(15), while having the observed value of  $\lambda$  be less than  $\lambda_1$  corresponds to  $\sigma < 0$ . Here  $\sigma = 0$  corresponds to  $\lambda = \lambda_1$ . Consequently, the model (10)-(11) predicts persistence when  $\lambda > \lambda_1$  and extinction when  $\lambda < \lambda_1$ . We base our analysis on (16)-(18) rather than on (13)-(15). We do so because we find it easier and more natural to relate  $\lambda$  ( and by extension  $d$ ) to the crucial demographic and biogeographic parameters  $r, L, \ell$ , and  $D$  of the model than we do  $\sigma$ .

The key observations regarding the eigenfunction  $w$  in (16)-(18) are that it is continuously differentiable on  $\mathbb{R}$  and that its form is determined on any interval upon which  $m(x)$  is constant. Consequently, if we set  $\alpha = \sqrt{\lambda_1}$ , then  $w(x)$  in (16)-(18) can be taken as:

$$\begin{cases} e^{\alpha x} & x < 0 \\ c_1 \cos(\alpha r x) + c_2 \sin(\alpha r x) & 0 < x < L \\ c_3 \cosh(\alpha(x-L)) + c_4 \sinh(\alpha(x-L)) & L < x < L+D \\ c_5 \cos(\alpha r(x-L-D)) + c_6 \sin(\alpha r(x-L-D)) & L+D < x < L+D+\ell \\ c_7 e^{-\alpha(x-L-D-\ell)} & x > L+D+\ell \end{cases}$$

where we have normalized  $w$  so that  $w(0) = 1$ . Matching  $w$  and its derivative across the interfaces at  $x = 0, L, L+D$ , and  $L+D+\ell$  enables us to determine that  $\alpha = \sqrt{\lambda_1}$  satisfies the transcendental equation  $\coth(\alpha D) =$

$$\frac{(r+1/r)^2 \sin(\alpha r \ell) \sin(\alpha r L) - (r-1/r) \sin(\alpha r(L+\ell)) + 2 \cos(\alpha r(L+\ell))}{[(r-1/r) \sin(\alpha r(L+\ell)) - 2 \cos(\alpha r(L+\ell))]} \quad (19)$$

2.1.3. *Analysis of the principal eigenvalue.* We now describe how (19) is analyzed to elucidate the dependence of the principal eigenvalue  $\lambda_1$  in (16) on the distance  $D$  between the two focal patches of habitat favorable to the species in question. We begin by observing for each  $r > 0$ , there is a unique  $\theta(r) \in (-\pi/2, \pi/2)$  so that  $\cos(\theta(r)) = \frac{2r}{r^2+1}$  and  $\sin(\theta(r)) = \frac{r^2-1}{r^2+1}$ ; namely,  $\theta(r) = \arcsin(\frac{r^2-1}{r^2+1})$ . Here  $\lim_{r \rightarrow 0^+} \theta(r) = -\pi/2$  and  $\lim_{r \rightarrow \infty} \theta(r) = \pi/2$ . Employing  $\theta(r)$ , we may re-write the right hand side of (19) as

$$\frac{(r+1/r) \sin(\alpha r L) \sin(\alpha r \ell)}{-\cos(\alpha r(L+\ell) + \theta(r))} - 1. \quad (20)$$

It is not difficult to check that (20) is negative for  $\alpha \in \left(0, \frac{\pi/2 - \theta(r)}{r(L+\ell)}\right)$ , where it has its first vertical asymptote. So if we let  $g(\alpha, r, L, \ell)$  denote (20),  $\lim_{\alpha \rightarrow \left[\frac{\pi/2 - \theta(r)}{r(L+\ell)}\right]^+} g(\alpha, r, L, \ell) = \infty$ . We may also observe that  $g(\alpha, r, L, \ell) = 1$  is equivalent to

$$\cos(\alpha r L + \theta(r)) \cos(\alpha r \ell + \theta(r)) = 0. \quad (21)$$

The smallest positive value of  $\alpha$  for which (21) holds is  $\alpha = \frac{\pi/2 - \theta(r)}{rL}$ . Consequently,  $g(\alpha, r, L, \ell) > 1$  for  $\alpha \in \left(\frac{\pi/2 - \theta(r)}{r(L+\ell)}, \frac{\pi/2 - \theta(r)}{rL}\right)$ . Since  $\lim_{\alpha \rightarrow 0^+} \coth(\alpha D) = +\infty$  and  $\lim_{\alpha \rightarrow +\infty} \coth(\alpha D) = 1$ , the smallest value of  $\alpha$  satisfying (20) lies in the interval.

We make a completely analogous analysis of the asymptotics of (10) in the case in which  $m(x)$  is replaced by  $\tilde{m}$ , where

$$\tilde{m}(x) = \begin{cases} -1 & x < 0 \\ r^2 & 0 < x < L \\ -1 & x > L \end{cases}$$

or

$$\tilde{m}(x) = \begin{cases} -1 & x < 0 \\ r^2 & 0 < x < L + \ell \\ -1 & x > L + \ell. \end{cases}$$

In this event, constructing the equation for  $\alpha$  is somewhat simpler, and one obtains that the smallest positive value  $\alpha_1$  satisfying the analogue of (19) is

$$\alpha_1 = \frac{\pi/2 - \theta(r)}{rL} \quad (\text{or } \frac{\pi/2 - \theta(r)}{r(L + \ell)}). \quad (22)$$

Consequently, the preceding discussion shows that for (10),  $\alpha_1 = \alpha_1(D, r, L, \ell)$  satisfies

$$\lim_{D \rightarrow 0^+} \alpha_1(D, r, L, \ell) = \frac{\pi/2 - \theta(r)}{r(L + \ell)} \quad (23)$$

$$\lim_{D \rightarrow \infty} \alpha_1(D, r, L, \ell) = \frac{\pi/2 - \theta(r)}{rL}.$$

Continuity of  $\alpha_1$  with respect to  $D$  and the fact that  $D$  does not appear explicitly in (20) allow us to conclude that  $g(\alpha, r, l, \ell)$  must be monotonically decreasing in  $\alpha$  in the interval  $(\frac{\pi/2 - \theta(r)}{r(L + \ell)}, \frac{\pi/2 - \theta(r)}{rL})$ . It then follows that  $\alpha_1 = \alpha_1(D, r, L, \ell)$  is strictly monotonically increasing in  $D$ .

*2.1.4. Model predictions.* We may now employ the preceding analysis of  $\lambda_1$  to describe the predictions of the reaction-diffusion formulation (10). Recall that  $d$  in (10) corresponds to  $1/\lambda$ , where  $\lambda$  is as in (16). Recall also that  $\theta(r) = \arcsin(\frac{r^2-1}{r^2+1})$ . So suppose now that  $d$  in (10) satisfies

$$\left(\frac{\pi/2 - \theta(r)}{r(L + \ell)}\right)^2 < 1/d < \left(\frac{\pi/2 - \theta(r)}{rL}\right)^2.$$

There is a unique  $D = D_{cr}$  so that

$$\alpha_1^2(D_{cr}, r, L, \ell) = 1/d.$$

$D_{cr}$  is then the threshold gap size between the two favorable patches. If the gap  $D$  between the two favorable patches is less than  $D_{cr}$ ,  $\alpha_1^2(D_{cr}, r, L, \ell) < 1/d$ . Consequently,  $\sigma > 0$  in (13)-(15) and the linear model (10) predicts persistence of the species in question. On the other hand, if  $D > D_{cr}$ ,  $\alpha_1^2(D_{cr}, r, L, \ell) > 1/d$ , which means  $\sigma < 0$  in (13)-(15) and (10) predicts the long term extinction of the species in question. If  $1/d > \left(\frac{\pi/2 - \theta(r)}{rL}\right)^2$ , it follows from (23) that the species in question is predicted to persist in an environment in which there is a single patch of length  $L$ . In this case (10) predicts the persistence of the species independent of how far apart the two favorable patches are. However, if  $1/d < \left(\frac{\pi/2 - \theta(r)}{r(L + \ell)}\right)^2$ , (10) predicts the eventual extinction of the species in question in an environment with a single favorable patch of length  $L + \ell$ .

## 2.2. Discrete-diffusion formulation.

*2.2.1. The model.* In order to approximate the model of the preceding subsection with a spatially implicit discrete-diffusion model, we envision five patches corresponding to the relevant subintervals of our one-dimensional universe. Thus patch 1 corresponds to the interval  $(\infty, 0]$ , patch 2 to  $[0, L]$ , patch 3 to  $[L, L + D]$ , patch 4 to  $[L + D, L + D + \ell]$ , and patch 5 to  $[L + D + \ell, \infty)$ . The state variable will now be a 5-tuple  $(u_1, u_2, u_3, u_4, u_5)$ , where  $u_i$  is a relevant representative density in patch  $i$ .



For patches 2, 3, and 4, it is natural to think of  $u_i$  as the average population density in patch  $i$  and  $U_i$  as the total population in patch  $i$ , so that  $U_2 = Lu_2$ ,  $U_3 = Du_3$ , and  $U_4 = \ell u_4$ . Since patches 1 and 5 correspond to intervals of infinite extent, it is no longer reasonable to think of total population as the product of average density and patch length. Instead, we appeal to the underlying reaction-diffusion equation, which is

$$u_t = du_{xx} - u \quad (24)$$

when  $x \in (-\infty, 0)$ ; i.e., when  $x$  is in patch 1. The bounded steady-state density for (24) is

$$u = u_1 e^{x/\sqrt{d}} \quad (25)$$

where  $u_1$  is the density at  $x = 0$ . From (25), the total population  $U_1$  in  $(-\infty, 0)$  is then given by

$$U_1 = \int_{-\infty}^0 u_1 e^{x/\sqrt{d}} dx = \sqrt{d} u_1.$$

Likewise, we have that the total population  $U_5$  in patch 5 is  $\sqrt{d} u_5$ , where  $u_5$  is the density at  $x = L + D + \ell$ . Mortality in patch 1 acts across the entire region leading to

$$\frac{dU_1}{dt} = -U_1. \quad (26)$$

Diffusive flux, however, acts locally at the interface between regions. Suppose that a population has density  $u(x, t)$  (in units of individuals/length). If individuals move by classical diffusion, diffusive flux, that is, the rate of transfer of individuals between the intervals  $(x - \Delta x, x)$  and  $(x, x + \Delta x)$  across an interface at  $x$ , should be given by

$$\frac{\delta}{\Delta t} [u(x - \Delta x, t)\Delta x - u(x, t)\Delta x]$$

where  $\delta$  is a dimensionless parameter. Now rewrite the preceding quantity as

$$\frac{\delta(\Delta x)^2}{\Delta t} \left[ \frac{u(x - \Delta x, t) - u(x, t)}{\Delta x} \right]$$

and define  $d = \frac{\delta(\Delta x)^2}{\Delta t}$ . The units of  $d$  are length squared/time. If we fix  $\frac{(\Delta x)^2}{\Delta t}$  and let  $\Delta x, \Delta t \rightarrow 0$ , we recover the usual flux  $J = -du_x$ , which leads to a standard diffusion equation  $u_t = du_{xx}$ . If we keep the same value of  $\frac{(\Delta x)^2}{\Delta t}$  and set  $\Delta x = 1$ , we obtain a transfer rate

$$\tilde{d}[u(x - \Delta x, t) - u(x, t)]$$

where  $\tilde{d} = \frac{d}{\Delta x}$  is numerically equal to  $d$  but has units length/time. In that which follows, we will drop the tilde on  $\tilde{d}$  since it is numerically equal to  $d$ . Other scalings are certainly possible, but our goal is to compare and contrast qualitative properties of different types of models, so the choice of scaling is not significant for our present purposes. Since the diffusive flux  $-d \nabla u$  is approximated by  $-d(u_2 - u_1)$ , adding dispersal to (26) yields

$$\frac{dU_1}{dt} = -U_1 + d(u_2 - u_1). \quad (27)$$

Our model therefore becomes

$$\begin{aligned}
\frac{du_1}{dt} &= -u_1 + \sqrt{d} (u_2 - u_1) \\
\frac{du_2}{dt} &= r^2 u_2 + \frac{d}{L} (u_1 - 2 u_2 + u_3) \\
\frac{du_3}{dt} &= -u_3 + \frac{d}{D} (u_2 - 2 u_3 + u_4) \\
\frac{du_4}{dt} &= r^2 u_4 + \frac{d}{\ell} (u_3 - 2 u_4 + u_5) \\
\frac{du_5}{dt} &= -u_5 + \sqrt{d} (u_4 - u_5).
\end{aligned} \tag{28}$$

2.2.2. *A possible alternative model.* Our formulation, as noted, assumes that the total species population in the matrix habitat between the two focal patches is the product of the average density there and the length  $D$  of the patch. An alternative would be to think of the total population as that which would arise from averaging the populations associated with decaying exponential equilibria emanating from each of the two focal habitats. Under this regime, the factor  $\frac{d}{D}$  in the third equation

of (28) becomes  $\frac{\sqrt{d}}{1 - e^{-D/\sqrt{d}}}$  so that (28) becomes

$$\begin{aligned}
\frac{du_1}{dt} &= -u_1 + \sqrt{d} (u_2 - u_1) \\
\frac{du_2}{dt} &= r^2 u_2 + \frac{d}{L} (u_1 - 2 u_2 + u_3) \\
\frac{du_3}{dt} &= -u_3 + \frac{\sqrt{d}}{1 - e^{-D/\sqrt{d}}} (u_2 - 2 u_3 + u_4) \\
\frac{du_4}{dt} &= r^2 u_4 + \frac{d}{\ell} (u_3 - 2 u_4 + u_5) \\
\frac{du_5}{dt} &= -u_5 + \sqrt{d} (u_4 - u_5).
\end{aligned} \tag{29}$$

As  $D \rightarrow 0$ ,  $\frac{\sqrt{d}}{1 - e^{-D/\sqrt{d}}} \rightarrow 1$ , and hence the predictions of (28) and (29) are essentially the same as  $D \rightarrow 0$ . However, as  $D \rightarrow \infty$ , (28) captures a far more pronounced denouement in the level of cooperation between the two focal patches than does (29). Consequently, we prefer and will consider the original formulation.

2.2.3. *Overview of model analysis.* In matrix form, (28) becomes

$$\begin{pmatrix} u_1 \\ u_2 \\ u_3 \\ u_4 \\ u_5 \end{pmatrix}' = \begin{pmatrix} -1 - \sqrt{d} & \sqrt{d} & 0 & 0 & 0 \\ \frac{d}{L} & r^2 - 2\frac{d}{L} & \frac{d}{L} & 0 & 0 \\ 0 & \frac{d}{D} & -1 - 2\frac{d}{D} & \frac{d}{D} & 0 \\ 0 & 0 & \frac{d}{\ell} & r^2 - 2\frac{d}{\ell} & \frac{d}{\ell} \\ 0 & 0 & 0 & \sqrt{d} & -1 - \sqrt{d} \end{pmatrix} \begin{pmatrix} u_1 \\ u_2 \\ u_3 \\ u_4 \\ u_5 \end{pmatrix}. \quad (30)$$

The off diagonal elements in (30) are nonnegative. Moreover, when a sufficiently large multiple of the  $5 \times 5$  identity matrix  $I_5$  is added to the matrix in (30), a nonnegative irreducible matrix results. So by [1], the matrix in (30) admits an eigenvector whose components are positive, corresponding to the largest real eigenvalue  $\sigma$ , which is necessarily simple. It is usual to refer to  $\sigma$  as the principal eigenvalue. When  $\sigma > 0$ , the zero equilibrium in (30) is unstable and a solution to (30) corresponding to componentwise positive initial data grows in all components. If  $\sigma < 0$ , the zero equilibrium is stable and solutions to (30) corresponding to componentwise positive initial data decay to 0 componentwise as time evolves.

Thus, to analyze (30), we need to examine the eigenvalues of the coefficient matrix. Our focus is expressing conditions for  $\sigma > 0$  or  $\sigma < 0$  in terms of tractable conditions on the demographic and geometric parameters of the problem, namely  $r, d, l, \ell$ , and  $D$ . In so doing, we are particularly interested in how conditions for  $\sigma > 0$  or  $\sigma < 0$  compare to conditions for the positivity or negativity of the principal eigenvalue in the case of the reduced model that arises when we think of having a single favorable patch of length  $L + \ell$ . In the case of a single favorable patch, (30) reduces to a 3-equation model

$$\begin{pmatrix} w_1 \\ w_2 \\ w_3 \end{pmatrix}' = \begin{pmatrix} -1 - \sqrt{d} & \sqrt{d} & 0 \\ \frac{d}{L + \ell} & r^2 - 2\frac{d}{L + \ell} & \frac{d}{L + \ell} \\ 0 & \sqrt{d} & -1 - \sqrt{d} \end{pmatrix} \begin{pmatrix} w_1 \\ w_2 \\ w_3 \end{pmatrix}. \quad (31)$$

The components  $w_1$  and  $w_3$  in (31) have the same meaning as  $u_1$  and  $u_5$  do in (30), respectively, while  $w_2$  has the same meaning as either  $u_2$  or  $u_4$  in (30).

The eigenvalues of the matrix in (31) are readily seen to be  $-1 - \sqrt{d} < 0$  and

$$\frac{1}{2} \left( r^2 - \frac{2d}{L + \ell} - 1 - \sqrt{d} \pm \sqrt{\left( r^2 - \frac{2d}{L + \ell} - 1 - \sqrt{d} \right)^2 + 4 \left( r^2 + r^2 \sqrt{d} - \frac{2d}{L + \ell} \right)} \right). \quad (32)$$

If  $r^2 + r^2 \sqrt{d} - \frac{2d}{L + \ell} > 0$ , it is immediate from (32) that the  $\sigma$  corresponding to the matrix in (31) is positive. Now

$$r^2 + r^2 \sqrt{d} - \frac{2d}{L+\ell} > 0 \Leftrightarrow L+\ell > \frac{2}{r^2 \left( \frac{1}{d} + \frac{1}{\sqrt{d}} \right)}.$$

Now if  $L+\ell \leq \frac{2}{r^2 \left( \frac{1}{d} + \frac{1}{\sqrt{d}} \right)}$ , then  $L+\ell < \frac{2}{\frac{r^2}{d}}$ , so that  $r^2 - \frac{2d}{L+\ell} < 0$ . It follows from (32) that the matrix in (31) does not have a positive eigenvalue. So we have that the  $\sigma$  in this case is positive if and only if  $L+\ell > \frac{2}{r^2 \left( \frac{1}{d} + \frac{1}{\sqrt{d}} \right)}$ . Hence

$\frac{2}{r^2 \left( \frac{1}{d} + \frac{1}{\sqrt{d}} \right)}$  is the threshold for a prediction of persistence in the case (31) of a single focal patch of favorable habitat of length  $L+\ell$ .

The eigenvalues for the coefficient matrix in (30) are the solutions to the determinantal equation

$$\begin{vmatrix} -1 - \sqrt{d} - \lambda & \sqrt{d} & 0 & 0 & 0 \\ \frac{d}{L} & r^2 - \frac{2d}{L} - \lambda & \frac{d}{L} & 0 & 0 \\ 0 & \frac{d}{D} & -1 - \frac{2d}{D} - \lambda & \frac{d}{D} & 0 \\ 0 & 0 & \frac{d}{\ell} & r^2 - 2\frac{d}{\ell} - \lambda & \frac{d}{\ell} \\ 0 & 0 & 0 & \sqrt{d} & -1 - \sqrt{d} - \lambda \end{vmatrix} = 0. \tag{33}$$

Since (30) is a  $5 \times 5$  system, it is far more difficult to express the eigenvalues of (30) in terms of the system parameters than it is to find the eigenvalues for the coefficient matrix of the  $3 \times 3$  system (31). Nevertheless, we are able to analyze (33) in the limiting cases as  $D \rightarrow 0$  and as  $D \rightarrow \infty$  with enough precision to compare to the case of a single favorable patch, as in (31).

2.2.4. *Analysis of the model as  $D \rightarrow 0$ .* One may readily show that for any  $D > 0$ , (33) is equivalent to

$$\begin{vmatrix}
 \frac{-1 - \sqrt{d} - \lambda}{d} & \frac{1}{\sqrt{d}} & 0 & 0 & 0 \\
 \frac{1}{L} & \frac{r^2}{d} - \frac{2}{L} - \frac{\lambda}{d} & \frac{1}{L} & 0 & 0 \\
 0 & \frac{1}{\sqrt{d}} & \frac{D + D\lambda + 2d}{-d^{3/2}} & \frac{1}{\sqrt{d}} & 0 \\
 0 & 0 & \frac{1}{\ell} & \frac{r^2}{d} - \frac{2}{\ell} - \frac{\lambda}{d} & \frac{1}{\ell} \\
 0 & 0 & 0 & \frac{1}{\sqrt{d}} & \frac{-1 - \sqrt{d} - \lambda}{d}
 \end{vmatrix}$$

= 0.

(34)

Now let  $D \rightarrow 0$ . The highest order term in the expansion in  $\lambda$  of (34) when  $D = 0$  is  $\frac{-2\lambda^4}{d^{9/2}}$ . Consequently, if the determinant in (34) is positive when  $D = 0$  and  $\lambda = 0$  (i.e., if the zero order term in the expansion of (34) in  $\lambda$  is positive when  $D = 0$ ), the principal eigenvalue of the matrix in (34) is positive when  $D = 0$ . In such a case, the zero order term in the expansion of (34) in  $\lambda$  remains positive for  $D$  positive and small by continuity. Since the highest order term in the expansion of (34) in  $\lambda$  when  $D > 0$  is  $\frac{-D\lambda^5}{d^{11/2}}$ , the principal eigenvalue of the matrix in (34) remains positive for  $D > 0$  and small. Since (33) and (34) have the same roots for  $D > 0$ , it follows that the  $\sigma$  associated with (30) is positive in this case.

The upshot of the previous discussion is that we want to determine conditions on the system parameters under which the determinant

$$\begin{vmatrix}
 \frac{-1}{d} - \frac{1}{\sqrt{d}} & \frac{1}{\sqrt{d}} & 0 & 0 & 0 \\
 \frac{1}{L} & \frac{r^2}{d} - \frac{2}{L} & \frac{1}{L} & 0 & 0 \\
 0 & \frac{1}{\sqrt{d}} & -\frac{2}{\sqrt{d}} & \frac{1}{\sqrt{d}} & 0 \\
 0 & 0 & \frac{1}{\ell} & \frac{r^2}{d} - \frac{2}{\ell} & \frac{1}{\ell} \\
 0 & 0 & 0 & \frac{1}{\sqrt{d}} & \frac{-1}{d} - \frac{1}{\sqrt{d}}
 \end{vmatrix}$$
(35)

is positive. A calculation shows that (35) equals

$$\begin{aligned} & \left(\frac{1}{d^{3/2}}\right)\left\{-\frac{2r^4}{d}\left(\frac{1}{d} + \frac{1}{\sqrt{d}}\right)^2 + r^2\left(\frac{1}{d} + \frac{1}{\sqrt{d}}\right)\left(\frac{3}{d} + \frac{1}{\sqrt{d}}\right)\left(\frac{1}{L} + \frac{1}{\ell}\right)\right. \\ & \quad \left.- 2\left(\frac{2}{d} + \frac{1}{\sqrt{d}}\right)\left(\frac{1}{L\ell}\right)\right\}. \end{aligned} \quad (36)$$

It is immediate that the sign of (36) is determined by the quantity

$$r^2\left(\frac{1}{d} + \frac{1}{\sqrt{d}}\right)\left(\frac{3}{d} + \frac{1}{\sqrt{d}}\right)(L + \ell) - \frac{2r^4}{d}\left(\frac{1}{d} + \frac{1}{\sqrt{d}}\right)^2 L\ell - 2\left(\frac{2}{d} + \frac{1}{\sqrt{d}}\right). \quad (37)$$

In the case of a single favorable patch of length  $L$  (or  $\ell$ ), we have that  $\sigma > 0 \Leftrightarrow L$  (or  $\ell$ )  $> \frac{2}{r^2\left(\frac{1}{d} + \frac{1}{\sqrt{d}}\right)}$ . Consequently, for the model (30) we assume

$$\ell \leq L < \frac{2}{r^2\left(\frac{1}{d} + \frac{1}{\sqrt{d}}\right)} \quad \text{but} \quad L + \ell > \frac{2}{r^2\left(\frac{1}{d} + \frac{1}{\sqrt{d}}\right)}. \quad (38)$$

It follows from (38) that

$$\frac{2}{r^2\left(\frac{1}{d} + \frac{1}{\sqrt{d}}\right)} < L + \ell < \frac{4}{r^2\left(\frac{1}{d} + \frac{1}{\sqrt{d}}\right)},$$

which is equivalent to

$$2 < r^2\left(\frac{1}{d} + \frac{1}{\sqrt{d}}\right)(L + \ell) < 4. \quad (39)$$

Let us think of  $k = r^2\left(\frac{1}{d} + \frac{1}{\sqrt{d}}\right)(L + \ell)$  as a parameter with a value between 2 and 4. Then

$$L = \frac{k}{r^2\left(\frac{1}{d} + \frac{1}{\sqrt{d}}\right)} - \ell. \quad (40)$$

Employing (40), we can re-write (37) in terms of  $\ell$  as

$$\begin{aligned} f_k(\ell) &= \left(\frac{3}{d} + \frac{1}{\sqrt{d}}\right)k - \frac{2r^4}{d}\left(\frac{1}{d} + \frac{1}{\sqrt{d}}\right)^2\left[\frac{k}{r^2\left(\frac{1}{d} + \frac{1}{\sqrt{d}}\right)} - \ell\right]\ell \\ & \quad - 2\left(\frac{2}{d} + \frac{1}{\sqrt{d}}\right) \\ &= \left(\frac{3}{d} + \frac{1}{\sqrt{d}}\right)k - \frac{2r^2k}{d}\left(\frac{1}{d} + \frac{1}{\sqrt{d}}\right)\ell + \frac{2r^4}{d}\left(\frac{1}{d} + \frac{1}{\sqrt{d}}\right)^2\ell^2 \\ & \quad - 2\left(\frac{2}{d} + \frac{1}{\sqrt{d}}\right). \end{aligned}$$

Here  $\ell \in [0, \frac{k}{2r^2\left(\frac{1}{d} + \frac{1}{\sqrt{d}}\right)}]$ . We have

$$\begin{aligned}
 f'_k(\ell) &= -\frac{2r^2k}{d}\left(\frac{1}{d} + \frac{1}{\sqrt{d}}\right) + \frac{4r^4}{d}\left(\frac{1}{d} + \frac{1}{\sqrt{d}}\right)^2\ell \\
 &= \frac{2r^2}{d}\left(\frac{1}{d} + \frac{1}{\sqrt{d}}\right)\left(-k + \frac{2r^2}{d}\left(\frac{1}{d} + \frac{1}{\sqrt{d}}\right)^2\ell\right) \\
 &\leq 0
 \end{aligned}$$

on  $\left[0, \frac{k}{2r^2\left(\frac{1}{d} + \frac{1}{\sqrt{d}}\right)}\right]$ . Consequently,

$$\begin{aligned}
 f_k(\ell) &\geq f_k\left(\frac{k}{2r^2\left(\frac{1}{d} + \frac{1}{\sqrt{d}}\right)}\right) \\
 &= \left(\frac{3}{d} + \frac{1}{\sqrt{d}}\right)k - \frac{k^2}{2d} - 2\left(\frac{2}{d} + \frac{1}{\sqrt{d}}\right) \\
 &= (k-2)\left(\frac{-k}{2d} + \frac{2}{d} + \frac{1}{\sqrt{d}}\right) \\
 &> 0
 \end{aligned}$$

for  $k \in (2, 4 + 2\sqrt{d})$ .

The preceding calculations and discussion show that if (38) holds, (35) is positive. Thus that the principal eigenvalue  $\sigma$  in (30) is positive for  $D > 0$  and small.

**Conclusion for (28) for  $D$  small under (38).** Hence, provided that (38) holds, the predictions of the spatially explicit reaction-diffusion model (10)-(11) when the distance  $D$  between favorable habitat patches is small can be captured qualitatively by the spatially implicit discrete-diffusion approximation (30).

2.2.5. *Analysis of the model as  $D \rightarrow 0$  when  $L + \ell = \frac{2}{r^2\left(\frac{1}{d} + \frac{1}{\sqrt{d}}\right)}$ .* Suppose now

that we consider the limiting situation that arises when (38) is replaced by

$$\ell \leq L < \frac{2}{r^2\left(\frac{1}{d} + \frac{1}{\sqrt{d}}\right)} \quad \text{with} \quad L + \ell = \frac{2}{r^2\left(\frac{1}{d} + \frac{1}{\sqrt{d}}\right)}. \quad (41)$$

Here (41) corresponds to

$$\frac{1}{d} = \left(\frac{\pi/2 - \theta(r)}{r(L + \ell)}\right)^2 \quad (42)$$

in the reaction-diffusion formulation of the model. Since the right hand side of (42) is (by (23)) the limit of  $\alpha_1^2(D, r, L, \ell)$  as  $d \rightarrow 0^+$  and since  $\alpha_1^2(D, r, L, \ell)$  is strictly increasing in  $D$ , (42) implies that  $\frac{1}{d} < \alpha_1^2(D, r, L, \ell)$  for any  $D$ . Consequently, if (42) holds,  $\sigma < 0$  in (10)-(11) for any  $D > 0$ , so that the reaction-diffusion model formulation predicts extinction when (42) holds for any  $D > 0$ . On the other hand, if (41) holds, we may substitute

$L = \gamma \left( \frac{2}{r^2 \left( \frac{1}{d} + \frac{1}{\sqrt{d}} \right)} \right)$  and  $\ell = (1 - \gamma) \left( \frac{2}{r^2 \left( \frac{1}{d} + \frac{1}{\sqrt{d}} \right)} \right)$ ,  $\gamma \in [1/2, 1)$ , directly into (37) and find that (37) reduces to

$$g(\gamma) \equiv \frac{1}{d}(2 - 8\gamma(1 - \gamma)). \quad (43)$$

It is elementary to check that  $g$  is increasing on  $[1/2, 1]$  with  $g(1/2) = 0$ . Thus  $g(\gamma) > 0$  in (43) if  $1/2 < \gamma < 1$ .

**Conclusion for (28) for  $D$  small under (41).** The quantity in (37) is positive when (41) holds if the two favorable patches are of different sizes. In this case, the discrete-diffusion patch model formulation predicts growth of the species in question when the gap size between the two favorable habitat patches is small, which is at odds with the predictions of the spatially explicit reaction-diffusion formulation. Consequently, our spatially implicit formulation is able to capture the predictions of the spatially explicit model as the gap size  $D$  tends to 0 closely but not precisely.

2.2.6. *Analysis of the model as  $D \rightarrow \infty$ .* Now suppose that the gap size  $D \rightarrow \infty$  in (30). In that case, the eigenvalue equation (33) reduces to

$$(-1 - \lambda) \begin{vmatrix} -1 - \sqrt{d} - \lambda & \sqrt{d} \\ \frac{d}{L} & r^2 - \frac{2d}{L} - \lambda \end{vmatrix} \begin{vmatrix} r^2 - \frac{2d}{\ell} - \lambda & \frac{d}{\ell} \\ \sqrt{d} & -1 - \sqrt{d} - \lambda \end{vmatrix} = 0. \quad (44)$$

As in the discussion of the eigenvalues of (31), (44) admits a positive  $\lambda$  if and only if  $L > \left( \frac{2}{r^2 \left( \frac{1}{d} + \frac{1}{\sqrt{d}} \right)} \right)$ . Now suppose that (38) or (41) hold, so that  $\ell \leq L <$

$\left( \frac{2}{r^2 \left( \frac{1}{d} + \frac{1}{\sqrt{d}} \right)} \right)$ . Then if  $\lambda$  is a root of (44),  $\lambda < 0$  or  $\lambda$  has negative real part.

Recall that for any  $D > 0$ , the matrix in (30) plus a sufficiently large multiple of the identity matrix is a nonnegative irreducible matrix. It follows that the matrix in (30) admits a largest real eigenvalue  $\sigma(D)$  with corresponding componentwise positive eigenvector. Moreover,  $\lambda = \sigma(D)$  is a simple root of (33). Consequently, the Implicit Function Theorem may be employed to guarantee that  $\sigma(D)$  is smooth in  $D$  for all  $D > 0$ . One may readily check that (33) is of the form

$$-\lambda^5 + (a_1 + \rho_1(1/D))\lambda^4 + (a_2 + \rho_2(1/D))\lambda^3$$

$$+ (a_3 + \rho_3(1/D))\lambda^2 + (a_4 + \rho_4(1/D))\lambda + (a_5 + \rho_5(1/D)) = 0$$

where  $\rho_i(0) = 0$  for  $i = 1, 2, 3, 4, 5$ . It follows that for any  $D^* > 0$ ,  $\sigma(D)$  is bounded uniformly on  $[D^*, \infty)$ . Thus for any sequence  $D_n \rightarrow \infty$ ,  $\sigma(D_n)$  has a subsequence which must converge to a root of (44). Since  $\sigma(D_n)$  is real valued for all  $n$ , this subsequence converges to a negative value. If  $\sigma(\infty)$  denotes the largest root of (44), then there can be no sequence  $D_n \rightarrow \infty$  so that  $\sigma(D_n) > \sigma(\infty)/2$  for all  $n$ .

**Conclusion for (28) when  $D \rightarrow \infty$ .** Thus if either (38) or (41) hold,  $\sigma(D) < 0$  for all sufficiently large values of  $D$ . So, in both the spatially explicit reaction-diffusion model formulation and the spatially implicit discrete-diffusion model formulation, there is a prediction of extinction of the species in question when the gap between the two favorable habitat patches is large, provided the sizes of the patches



are below the threshold size for a prediction of growth in the situation where there is only a single favorable habitat patch.

2.2.7. *Can the discrete-diffusion model (28) be reduced?* A variant on the discrete-diffusion formulation of the model would be to consider only the two favorable habitat patches and the unfavorable territory between them, ignoring the loss to the surrounding environs. This reduction leads to the model

$$\begin{pmatrix} z_1 \\ z_2 \\ z_3 \end{pmatrix}' = \begin{pmatrix} r^2 - \frac{d}{L} & \frac{d}{L} & 0 \\ \frac{d}{D} & -1 - \frac{2d}{D} & \frac{d}{D} \\ 0 & \frac{d}{\ell} & r^2 - \frac{d}{\ell} \end{pmatrix} \begin{pmatrix} z_1 \\ z_2 \\ z_3 \end{pmatrix}. \quad (45)$$

The components  $z_1$  and  $z_3$  in (45) correspond to  $u_2$  and  $u_4$  in (30), respectively, while  $z_2$  has the same meaning as  $u_3$  in (30).

The eigenvalues for the coefficient matrix in (45) are given by the solutions to

$$\begin{vmatrix} r^2 - \frac{d}{L} - \lambda & \frac{d}{L} & 0 \\ \frac{d}{D} & -1 - \frac{2d}{D} - \lambda & \frac{d}{D} \\ 0 & \frac{d}{\ell} & r^2 - \frac{d}{\ell} - \lambda \end{vmatrix} = 0. \quad (46)$$

A direct calculation shows that (46) reduces to

$$-2d(r^2 - \lambda)(r^2 - 1/2(\frac{d}{\ell} + \frac{d}{L}) - \lambda) + D(r^2 - \frac{d}{L} - \lambda)(-1 - \lambda)(r^2 - \frac{d}{\ell} - \lambda) = 0. \quad (47)$$

Notice that if  $\lambda = r^2$ , the left hand side of (47) becomes  $-D\frac{d^2}{L\ell}(1 + r^2)$  which is negative. However, for any fixed  $\lambda \in (r^2 - 1/2(\frac{d}{\ell} + \frac{d}{L}), r^2)$ , the left hand side is positive for all sufficiently small values of  $D$ . Consequently,  $\sigma(D) > 0$  for small values of  $D$ , independent of the sizes of  $L$  and  $\ell$ . On the other hand, consider (45) when  $D$  is large. If  $L < \frac{d}{r^2}$ , one may show that  $\sigma(D) < 0$  for (45) for all sufficiently large values of  $D$ . (Here the argument is analogous to that given for  $\sigma(D)$  for (30) when (38) holds.) However, if  $L > \frac{d}{r^2}$  and  $\lambda \in (\max\{0, r^2 - \frac{d}{\ell}\}, r^2 - \frac{d}{L})$ , then the left hand side of (47) is positive if  $D$  is sufficiently large. Therefore, since the leading term of the left hand side of (47) is  $-D\lambda^3$ ,  $\sigma(D) > 0$  for (45) for all sufficiently large  $D$ .

**Conclusions for the reduced model (45).** Since it predicts persistence for  $D$  small independent of the sizes of  $L$  and  $\ell$ , (45) is not realistic as an approximation to the reaction-diffusion formulation (10)-(11) of the model when  $D \rightarrow 0$ . In this instance the phenomena captured by (45) more closely resemble those that obtain when (10) is set on  $(0, L + D + \ell) \times (0, \infty)$  subject to homogeneous Neumann boundary data where

$$m(x) = \begin{cases} r^2 & 0 < x < L \\ -1 & L < x < L + D \\ r^2 & L + D < x < L + D + \ell. \end{cases}$$

On the other hand, the reduced model (45) predicts growth (respectively extinction) when the gap between the two favorable patches is large provided the larger favorable patch is strictly above (respectively strictly below) a threshold, which is also the case in the reaction-diffusion formulation.

2.2.8. *Conclusions for discrete-diffusion models.* When  $D \rightarrow \infty$ , the (28) and (45) exhibit the same qualitative features as the reaction-diffusion model (10) - (11). Specifically, they predict persistence under the condition that a population could persist on the larger patch in isolation and extinction otherwise. As  $D \rightarrow 0$ , the predictions of (45) do not agree with those of (10)-(11) in that (45) predicts persistence when  $D$  is sufficiently small for positive values of  $L$  and  $\ell$ . When (38) holds, so that  $L + \ell$  is larger than the minimal threshold length needed for a single patch in isolation to support a population, then the prediction of (28) is qualitatively the same as that of (10)-(11). However, when  $L + \ell$  is equal to the minimal threshold length, the prediction of (28) as  $D \rightarrow 0$  is qualitatively the same as that of (10)-(11) if  $L = \ell$  but not when  $L \neq \ell$ . When  $L \neq \ell$ , (28) predicts persistence for  $D$  small while (10)-(11) does not.

### 3. Integro-difference versus average dispersal success formulation.

#### 3.1. Integro-difference formulation.

3.1.1. *The model.* Here the state variable  $u$  has the same meaning as in the reaction-diffusion formulation of the model. Namely,  $u$  denotes the population density of a species along a one-dimensional axis of infinite extent. As before, the axis contains two finite patches of habitat favorable to the population, separated and surrounded by habitat unfavorable to the species. Once again, the lengths of the favorable patches are  $L$  and  $\ell$ , with  $\ell \leq L$ , and the length of the patch of unfavorable habitat separating them is  $D$ . As in the preceding section, we assume that the favorable patches are located between 0 and  $L$  and between  $L + D$  and  $L + D + \ell$  on a number line.

The model in this context corresponding to (10)-(11) in the reaction-diffusion formulation is

$$u_{t+1}(x) = \int_{-\infty}^{\infty} k(x, y) m(y) u_t(y) dy. \quad (48)$$

In (48),  $k(x, y)$  is the dispersal kernel, representing the likelihood of successfully dispersing from point  $y$  to point  $x$  during a single time step, and  $m(y)$  is the local intrinsic growth rate at  $y$ . In the integro-difference context, local growth at  $y$  corresponds to  $m(y) > 1$  while local decline at  $y$  corresponds to  $0 < m(y) < 1$ . Consequently, in order to parallel our treatment in the reaction-diffusion formulation, we assume

$$m(y) = \begin{cases} e^{-s} & y < 0 \\ e^r & 0 < y < L \\ e^{-s} & L < y < L + D \\ e^r & L + D < y < L + D + \ell \\ e^{-s} & y > L + D + \ell, \end{cases} \quad (49)$$

where  $r > 0$  and  $s > 0$ .

3.1.2. *Principal eigenvalues.* The eigenvalue problem for (48) corresponding to (13)-(15) in the reaction-diffusion setting is

$$\lambda \phi(x) = \int_{-\infty}^{\infty} k(x, y) m(y) \phi(y) dy, \quad (50)$$

where  $\phi(x) > 0$  on  $(-\infty, \infty)$  and  $\lim_{x \rightarrow \pm\infty} \phi(x) = 0$ . Provided that (50) admits such a solution, the solution to the linear problem (48) with  $u_0(x) = \alpha \phi(x)$  ( $\alpha > 0$ ) is

$$u_n(x) = \alpha \lambda^n \phi(x) \quad (51)$$

so that (48) predicts growth when  $\lambda > 1$  and decline when  $\lambda < 1$ . As in the previous section, we denote such a  $\lambda$  when it exists by  $\lambda_1$ .

3.1.3. *Analysis of the principal eigenvalue- Overview.* Our approach to (50) borrows heavily from Van Kirk and Lewis [12]. In that paper, the underlying spatial habitat is a bounded set  $\Omega$ , in which case the analogue to the right hand side of (48) is a compact linear operator on  $L^2(\Omega)$ , for example. Such will not be the case in general for  $\Omega = (-\infty, \infty)$ , and thus we can not make an analogous appeal to the spectral theory of compact operators to examine the eigenvalue problem (50). However, Van Kirk and Lewis show that in the special but widely considered case of the Laplace or exponential kernel

$$k(x, y) = k(x - y) = 1/2 e^{-|x-y|} \quad (52)$$

the analogue to (50) is equivalent to a two point boundary value problem for a second order elliptic problem on a bounded interval. This tactic carries over to the case where  $\Omega = (-\infty, \infty)$ , so that if  $k$  and  $m$  in (50) are given by (52) and (49), respectively, (50) is equivalent to having  $\phi(x) > 0$  on  $(-\infty, \infty)$  with

$$\phi''(x) = \begin{cases} (1 - \frac{e^{-s}}{\lambda}) \phi(x) & x < 0, L < x < L + D, x > L + D + \ell \\ (1 - \frac{e^r}{\lambda}) \phi(x) & 0 < x < L, L + D < x < L + D + \ell \end{cases} \quad (53)$$

and  $\phi(x) \rightarrow 0$  as  $x \rightarrow \pm\infty$ .

Regarding (53), we may establish that for each  $D \geq 0$ , there is a unique  $\lambda = \lambda(D) \in (e^{-s}, e^r)$  so that (53) is solvable, and moreover that  $\lambda$  is continuous and strictly decreasing as a function of  $D$ . As a consequence, if there is a value  $D_{cr} > 0$  so that  $\lambda(D_{cr}) = 1$ , we have that (48) predicts growth if  $D < D_{cr}$  and extinction if  $D > D_{cr}$ .

3.1.4. *Employing Brown et al [2].* Observe that if  $\lambda \in (e^{-s}, e^r)$ , (53) can be incorporated into the framework of Brown et al [2]. Namely, if  $\lambda \in (e^{-s}, e^r)$ , the function  $\tilde{m}(x, \lambda)$  given by

$$\tilde{m}(x, \lambda) = \begin{cases} \frac{e^{-s}}{\lambda} - 1, & x < 0 \\ \frac{e^r}{\lambda} - 1, & 0 < x < L \\ \frac{e^{-s}}{\lambda} - 1, & L < x < L + D \\ \frac{e^r}{\lambda} - 1, & L + D < x < L + D + \ell \\ \frac{e^{-s}}{\lambda} - 1, & x > L + D + \ell \end{cases}$$

is such that the eigenvalue problem

$$-\phi''(x) = \mu \tilde{m}(x, \lambda) \phi(x) \quad (54)$$

in  $(-\infty, \infty)$  with

$$\phi(x) \rightarrow 0 \text{ as } x \rightarrow \pm\infty \quad (55)$$

has a unique positive principal eigenvalue  $\mu$  with corresponding eigenfunction  $\phi > 0$ . Here  $\mu = \mu(\lambda)$  and  $\mu(\lambda) = 1$  is equivalent to  $\lambda$  being an eigenvalue for (50).

Our candidate for a positive solution  $\phi(x)$  of (53) is given by

$$\left\{ \begin{array}{ll} \exp(\sqrt{1 - \frac{e^{-s}}{\lambda}} x), & x < 0 \\ c_1 \cos(\sqrt{\frac{e^r}{\lambda} - 1} x) + c_2 \sin(\sqrt{\frac{e^r}{\lambda} - 1} x), & 0 < x < L \\ c_3 \cosh(\sqrt{1 - \frac{e^{-s}}{\lambda}} (x - L)) + c_4 \sinh(\sqrt{1 - \frac{e^{-s}}{\lambda}} (x - L)), & L < x < L + D \\ c_5 \cos(\sqrt{\frac{e^r}{\lambda} - 1} (x - L - D)) + c_6 \sin(\sqrt{\frac{e^r}{\lambda} - 1} (x - L - D)), & L + D < x < L + D + \ell \\ c_7 \exp(-\sqrt{1 - \frac{e^{-s}}{\lambda}} (x - L - D - \ell)), & x > L + D + \ell. \end{array} \right. \quad (56)$$

3.1.5. *Analysis of the transcendental equation for  $\lambda_1$ .* Embedding (53) into (54)-(55) will enable us to invoke the results of [2] to guarantee a univque positive eigenvalue  $\lambda_1$  of (50). To this end, the form in (56) arises from the piecewise nature of the definition of  $\tilde{m}(x, \lambda)$  and the requirement that  $\phi(x) \rightarrow 0$  as  $x \rightarrow \pm\infty$ . Requiring that  $\phi$  be continuously differentiable then leads to an equation for  $\lambda_1$ , namely

$$\coth\left(\sqrt{1 - \frac{e^{-s}}{\lambda}} D\right) = \frac{(e^r - e^{-s}) \sin\left(\sqrt{\frac{e^r}{\lambda} - 1} L\right) \sin\left(\sqrt{\frac{e^r}{\lambda} - 1} \ell\right)}{\sqrt{(\lambda - e^{-s})(e^r - \lambda)} \left(-\cos\left(\sqrt{\frac{e^r - \lambda}{\lambda}}(L + \ell) + \arcsin\left(\frac{e^r - 2\lambda + e^{-s}}{e^r - e^{-s}}\right)\right)\right)} - 1 \quad (57)$$

or equivalently

$$\sqrt{\lambda - e^{-s}} \coth\left(\sqrt{1 - \frac{e^{-s}}{\lambda}} D\right) + \sqrt{\lambda - e^{-s}} = \frac{(e^r - e^{-s}) \sin\left(\sqrt{\frac{e^r}{\lambda} - 1} L\right) \sin\left(\sqrt{\frac{e^r}{\lambda} - 1} \ell\right)}{\sqrt{(e^r - \lambda)} \left(-\cos\left(\sqrt{\frac{e^r - \lambda}{\lambda}}(L + \ell) + \arcsin\left(\frac{e^r - 2\lambda + e^{-s}}{e^r - e^{-s}}\right)\right)\right)} \quad (58)$$

In order to delineate (57) or (58), we need to examine the special case when  $D = 0$  and we have a single patch of length  $L + \ell$  of favorable habitat. In this case, the local growth rate function  $m(y)$  is just

$$m(y) = \begin{cases} e^{-s} & y < 0 \\ e^r & 0 < y < L + \ell \\ e^{-s} & y > L + \ell. \end{cases}$$

We can now exploit the fact that we have spatial symmetry about the center of the favorable habitat to translate the problem (53) so that  $x = 0$  corresponds to the center of the favorable patch. In so doing, we need only consider  $[0, \infty)$ , and the form of  $\phi(x)$  may be taken as

$$\phi(x) = \begin{cases} \cos\left(\sqrt{\frac{e^r}{\lambda} - 1} x\right), & 0 \leq x \leq \frac{L + \ell}{2} \\ c_1 \exp\left(-\sqrt{1 - \frac{e^{-s}}{\lambda}} \left(x - \frac{L + \ell}{2}\right)\right), & x \geq \frac{L + \ell}{2}. \end{cases} \quad (59)$$

As was the case with (56), the requirement that  $\phi(x)$  be continuously differentiable leads to an equation for  $\lambda$ . In this case,  $\lambda$  must satisfy

$$\tan\left(\sqrt{\frac{e^r}{\lambda} - 1} \left(\frac{L + \ell}{2}\right)\right) = \sqrt{\frac{\lambda - e^{-s}}{e^r - \lambda}}. \quad (60)$$

It is straightforward to see that (60) has a unique solution  $\bar{\lambda} \in (\max\{\lambda^*, e^{-s}\}, e^r)$ , where  $\lambda^*$  is the unique positive value of  $\lambda$  for which

$\sqrt{\frac{e^r}{\lambda} - 1} \left(\frac{L + \ell}{2}\right) = \frac{\pi}{2}$ . Moreover, in this case  $\phi$  in (59) is positive. Hence (53) admits a positive solution, meaning that  $\bar{\lambda} = \lambda(0)$  and  $1 = \mu(\lambda(0))$  in (54)-(55).

Since

$$\sqrt{\frac{e^r}{\lambda(0)} - 1} \left(\frac{L + \ell}{2}\right) < \frac{\pi}{2},$$

$$\lambda(0) > e^r \frac{(L + \ell)^2}{(L + \ell)^2 + \pi^2} \quad (61)$$

so that  $\lambda(0) > 1$  provided either  $L + \ell$  or  $e^r$  is large enough.

One may readily check that  $\bar{\lambda} = \lambda(0)$  is the largest value of  $\lambda \in (e^{-s}, e^r)$  for which the right hand side of (58) has a singularity. Moreover, if we denote the right hand side of (58) by  $g^*(\lambda)$ , then  $\lim_{\lambda \rightarrow \bar{\lambda}^-} g^*(\lambda) = +\infty$ ,  $\lim_{\lambda \rightarrow \bar{\lambda}^+} g^*(\lambda) = -\infty$  and  $g^*(\lambda) < 0$  for  $\lambda \in (\bar{\lambda}, e^r]$ . As a consequence,  $\lambda(0)$  is an upper bound on any  $\lambda$  that would admit a positive solution to (53) for any  $D > 0$ . On the other hand, if  $\phi$  is to

be positive in (53) for some choice of  $\lambda$ , it follows from (56) that  $\sqrt{\frac{e^r}{\lambda} - 1} L < \pi$

so that  $\lambda > e^r \left( \frac{L^2}{L^2 + \pi^2} \right)$ . So for any  $D > 0$ , if  $\lambda(D)$  exists, then

$$e^r \left( \frac{L^2}{L^2 + \pi^2} \right) < \lambda(D) < \lambda(0). \quad (62)$$

Note also that  $e^r \left( \frac{L^2}{L^2 + \pi^2} \right)$  is the largest value of  $\lambda \in (0, e^r)$  for which  $g^*(\lambda) = 0$ .

In order to establish the existence of  $\lambda(D)$ , we need to sharpen the lower bound in (62). Any positive solution to (53) is necessarily a decaying exponential at  $\pm\infty$ . With this observation in mind, differential equation arguments based on Green's Second Identity may be employed to show that if  $L, \ell, D, r$  and  $s$  are fixed, there can be at most one value of  $\lambda$  so that (53) admits a positive solution. The natural expectation would be that this value of  $\lambda$  is the largest value of  $\lambda \in (e^{-s}, \lambda(0))$  for which (58) holds. One may show that the left hand side of (58) is a uniformly continuous, bounded, positive function on  $(e^{-s}, \lambda(0))$ , so that there is a largest  $\lambda \in (e^{-s}, \lambda(0))$  satisfying (58). Since the left hand side of (58) exceeds  $2\sqrt{\lambda - e^{-s}}$  for any  $D > 0$ , this largest  $\lambda$  must exceed the largest root of

$$\frac{(e^r - e^{-s}) \sin\left(\sqrt{\frac{e^r}{\lambda} - 1} L\right) \sin\left(\sqrt{\frac{e^r}{\lambda} - 1} \ell\right)}{\sqrt{(e^r - \lambda)(\lambda - e^{-s})} \left(-\cos\left(\sqrt{\frac{e^r - \lambda}{\lambda}}(L + \ell) + \arcsin\left(\frac{e^r - 2\lambda + e^{-s}}{e^r - e^{-s}}\right)\right)\right)} = 2. \quad (63)$$

Let  $\bar{\lambda}$  denote the largest root of (63). One may show that  $\bar{\lambda}$  satisfies

$$\tan\left(\sqrt{\frac{e^r}{\lambda} - 1} \frac{L}{2}\right) = \sqrt{\frac{\lambda - e^{-s}}{e^r - \lambda}}. \quad (64)$$

Notice from (60) that (64) is the equation for the eigenvalue  $\lambda$  in (53) when there is a single favorable habitat patch of length  $L$ . Consequently,  $\bar{\lambda} >$

$\max\left\{\frac{L^2}{L^2 + \pi^2} e^r, e^{-s}\right\}$  and the left hand side of (63) exceeds 2 for  $\lambda \in (\bar{\lambda}, \lambda(0))$ .

Recall now that (58) is equivalent to (57). Let  $g(\lambda)$  denote the right hand side of (57). The preceding observation shows that  $g(\lambda) > 1$  on  $(\bar{\lambda}, \lambda(0))$ , so that (57) is equivalent to

$$D = 1/2 \sqrt{\frac{\lambda}{\lambda - e^{-s}}} \ln\left(\frac{g(\lambda) + 1}{g(\lambda) - 1}\right). \quad (65)$$

Since  $\lim_{\lambda \rightarrow \lambda(0)^-} g(\lambda) = +\infty$ , the right hand side of (65) tends to 0 as  $\lambda \rightarrow \lambda(0)^-$ . Since  $\lim_{\lambda \rightarrow \bar{\lambda}^+} g(\lambda) = 1$ , the right hand side of (65) tends to  $+\infty$  as  $\lambda \rightarrow \bar{\lambda}^+$ .

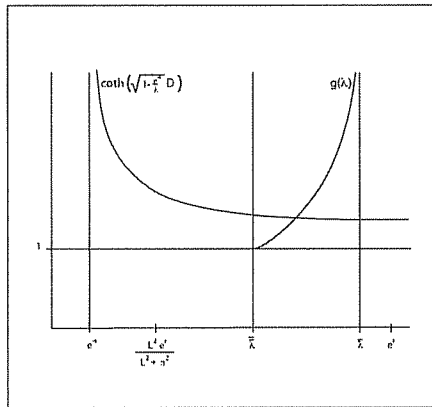


FIGURE 1. Schematic illustrating the solution of (57). The left hand side is a monotonically decreasing function of  $\lambda$  on  $(e^{-s}, e^r)$  which approaches  $\infty$  as  $\lambda \rightarrow e^{-s}$  and exceeds 1 throughout  $(e^{-s}, e^r)$ . The right hand side takes the value 1 at  $\lambda = \bar{\lambda}$  and exceeds 1 on the interval  $(\bar{\lambda}, \tilde{\lambda})$  with  $\lim_{\lambda \rightarrow \tilde{\lambda}^-} g(\lambda) = +\infty$ . Here  $\bar{\lambda}$  is the principal eigenvalue for (50) in the case in which there is a single favorable habitat of length  $L + \ell$ , while  $\tilde{\lambda}$  is the principal eigenvalue for (50) when there is a single favorable habitat patch of length  $L$ .

So now use (65) to define  $D(\lambda)$  for  $\lambda \in (\bar{\lambda}, \lambda(0)]$ , with  $D(\lambda(0)) = 0$  and consider  $\tilde{m}(x, \lambda)$  with  $D = D(\lambda)$ . We may show that for  $\lambda \in (\bar{\lambda}, \lambda(0)]$ ,  $\mu \equiv 1$  in

$$\begin{aligned} \phi''(x) &= \mu \tilde{m}(x, \lambda) \phi \quad \text{on } (-\infty, \infty) \\ \phi &> 0 \quad \text{on } (-\infty, \infty) \end{aligned} \tag{66}$$

$$\phi \rightarrow 0 \quad \text{as } x \rightarrow \pm \infty.$$

To this end,  $\lambda \rightarrow \tilde{m}(x, \lambda)$  is continuous from  $(\bar{\lambda}, \tilde{\lambda}]$  into  $L^p_{loc}(\mathbb{R})$  for any  $p \in [1, \infty)$ , so that  $\lambda \rightarrow \mu(\lambda)$  is a continuous map from  $(\bar{\lambda}, \tilde{\lambda}]$  into  $\mathbb{R}$ . We have shown that  $\mu = 1$  in (54) when  $\lambda = \bar{\lambda}$  and hence that  $D(\bar{\lambda}) = 0$ . Indeed, in this case, we have shown that the function  $\phi$  which arises from matching function and derivative values across interfaces is positive on  $\mathbb{R}$ . Moreover, the functions  $\phi(\lambda)$  which we construct by the matching process with  $D = D(\lambda) > 0$  have the property that  $\phi(\lambda) \rightarrow \phi(\bar{\lambda})$  uniformly on any bounded subset of  $\mathbb{R}$  as  $\lambda \rightarrow \bar{\lambda}$ . In particular, we have uniform convergence on  $[a, b]$  where  $a < 0$  is arbitrary and  $b > L + \ell$ . It follows that for  $\lambda$  close enough to  $\bar{\lambda}$ ,  $L + \ell + D(\lambda) < b$  and  $\phi(\lambda)$  is positive on  $[a, b]$ . Since  $\tilde{m}(x, \lambda) = \frac{e^{-s}}{\lambda} - 1$  on  $(-\infty, 0) \cup (L + \ell + D(\lambda), \infty)$ , it must be the case that  $\phi(\lambda)$  is in fact positive on  $\mathbb{R}$  for  $\lambda$  close enough to  $\bar{\lambda}$ . So  $\mu(\lambda) = 1$  for all

$\lambda$  close enough to  $\bar{\lambda}$ . Hence we have that  $\mu(\lambda) = 1$  with eigenfunction  $\phi(\lambda) > 0$  on  $\mathbb{R}$  for  $\lambda \in (\bar{\lambda}, \bar{\lambda})$  for some  $\bar{\lambda} < \bar{\lambda}$ . Since  $\phi(\lambda) > 0$  on  $\mathbb{R}$  for  $\lambda \in (\bar{\lambda}, \bar{\lambda})$ , it follows that  $\phi(\bar{\lambda}) \geq 0$  on  $\mathbb{R}$ . From its construction  $\phi(\bar{\lambda})$  is not identically 0. Since  $\phi''(x) - \phi(x) \leq 0$  on  $[a, b]$  for  $a < 0$  and  $L + \ell + D(\bar{\lambda}) < b$ , the maximum principle implies that  $\phi(\bar{\lambda}) > 0$  on  $[a, b]$  and thus on  $\mathbb{R}$ . It follows that  $\phi(\bar{\lambda})$  is a positive solution of (53). Consequently,  $\mu(\bar{\lambda}) = 1$ . We may now repeat the argument to obtain that  $\mu(\lambda) \equiv 1$  on  $(\bar{\lambda}, \bar{\lambda}]$  with  $\phi(\lambda)$  constructed according to the matching procedure.

Now  $D(\lambda)$  in (65) is continuous in  $\lambda$  for  $\lambda \in (\bar{\lambda}, \bar{\lambda}]$ . As noted, differential equations arguments based on Green's Second Identity show that if  $\ell, L, D, r$  and  $s$  are fixed, there can be at most one value of  $\lambda$  so that (53) admits a positive solution. As a result  $D(\lambda_1) \neq D(\lambda_2)$  if  $\lambda_1 \neq \lambda_2$ . Consequently,  $D(\lambda)$  in (65) is injective and from context strictly decreasing in  $\lambda$ . We may thus solve (65) for  $\lambda$  in terms of  $D$  for  $D \geq 0$ . The resulting  $\lambda(D)$  is the unique value of  $\lambda$  in  $(e^{-s}, e^r)$  for which (53) (and hence (50)) admits a positive solution  $\phi$ . Note that  $\lambda(D) \rightarrow \bar{\lambda}$  as  $D \rightarrow 0$ , where  $\bar{\lambda}$  is the unique value of  $\lambda$  for which (53) admits a positive solution  $\phi$  when there is a single favorable habitat patch of length  $L + \ell$ , and that  $\lambda(D) \rightarrow \bar{\lambda}$  as  $D \rightarrow \infty$ , where  $\bar{\lambda}$  is the unique value of  $\lambda$  for which (53) admits a positive solution  $\phi$  when there is a single favorable habitat patch of length  $L$ .

**3.1.6. Model predictions.** We have now shown that for each  $D \geq 0$ , there is a unique  $\lambda_1(D) > 0$  so that (53) admits a positive solution and thus  $\lambda_1(D) > 0$  is the unique eigenvalue of (50) admitting a positive solution. Moreover,  $\lambda_1(D)$  is strictly increasing as a function of  $D$ . Consequently, if  $\bar{\lambda} > 1$  in (60) and  $\bar{\lambda} < 1$  in (64), there is a unique critical value  $D_{cr} > 0$  so that  $\lambda_1(D_{cr}) = 1$ . Thus (48) predicts growth if  $0 \leq D < D_{cr}$  and extinction if  $D > D_{cr}$ .

## 3.2. Average dispersal success formulation.

**3.2.1. The model.** The idea of an average dispersal success approximation to an integro-

difference model of the form (48) was introduced in VanKirk and Lewis [12] and built upon in Lutscher and Lewis [10] and Fagan and Lutscher [5]. In this approach, the linear integro-difference model (50) is replaced by a matrix equation in  $\mathbb{R}^n$ , where  $n$  is the number of focal patches under consideration. As formulated in [12], the average dispersal success approximation requires each focal patch to be bounded in extent (i.e., to have finite length, area or volume), reflecting a situation in which one regards "dispersal events, that are, on some scale, philopatric as successful and those that are non-philopatric as unsuccessful (i.e., success is viewed from the perspective of the source population)" [5]. Since the local growth rate in the integro-difference model (48) is  $e^{-s} < 1$  for  $x < 0$  or  $x > L + D + \ell$ , regions away from the focal patches are deemed unsuitable for the species in question. Thus we follow [12] (p. 110) and truncate the exponential kernel (52) outside a finite spatial range. It certainly should be possible to employ the fact the species density decays to zero away from the focal patches to accommodate exterior patches of infinite extent, as we did in Section 2.2, but we have not done so at this time.

In the case of a single focal patch  $\Omega$  of finite extent and an integro-difference model of the form



$$u(x, t + 1) = \int_{\Omega} k(x, y) e^r u(y, t) dy \quad (67)$$

where  $k$  is the dispersal kernel and  $e^r$  is a constant growth rate, the average dispersal success formulation replaces  $u(y, t)$  in (67) with its average density

$$\bar{u}(t) = \frac{1}{|\Omega|} \int_{\Omega} u(z, t) dz$$

and replaces the dispersal kernel  $k(x, y)$  with its average rate of arrival into  $\Omega$  from  $y$ , namely

$$\bar{k}(y) = \frac{1}{|\Omega|} \int_{\Omega} k(x, y) dx$$

and thus considers the model

$$\begin{aligned} \bar{u}(t + 1) &= e^r \int_{\Omega} \int_{\Omega} \left( \frac{1}{|\Omega|} k(x, y) dx \right) \int_{\Omega} \left( \frac{1}{|\Omega|} u(z, t) dz \right) dy \\ &= \frac{e^r}{|\Omega|} \left( \int_{\Omega} \int_{\Omega} k(x, y) dx dy \right) \bar{u}(t) \end{aligned} \quad (68)$$

in place of (67). When multiple focal patches  $\Omega_i, i = 1, \dots, n$  are considered, following [5] and [10], we obtain

$$\bar{u}_i(t + 1) = \sum_{j=1}^n e^{r_j} \left( \frac{1}{|\Omega_i|} \int_{\Omega_i} \int_{\Omega_j} k(x, y) dy dx \right) \bar{u}_j(t) \quad (69)$$

The term  $p_{ij} = \frac{1}{|\Omega_i|} \int_{\Omega_i} \int_{\Omega_j} k(x, y) dy dx$  in (69) gives the average rate of arrival into  $\Omega_i$  from  $y$  in  $\Omega_j$ , integrated over all  $y \in \Omega_j$ .

Here we use the average dispersal success approximation as a surrogate for the integro-difference formulation in Subsection 3.1 in three ways. First we view  $\Omega = (0, L) \cup (L + D, L + D + \ell)$  as a single patch, then we view  $(0, L) \cup (L + D, L + D + \ell)$  as two patches, with  $\Omega_1 = (0, L)$  and  $\Omega_2 = (L + D, L + D + \ell)$ , and finally we consider three patches, with  $\Omega_1 = (0, L)$ ,  $\Omega_2 = (L, L + D)$  and  $\Omega_3 = (L + D, L + D + \ell)$ .

**3.2.2. Model predictions when favorable habitat is viewed as a single patch.** When we view the favorable regions of habitat as a single patch  $\Omega_D = (0, L) \cup (L + D, L + D + \ell)$ , the length  $|\Omega_D| = L + \ell$  for all  $D$ . So (68) becomes

$$\begin{aligned} \bar{u}(t + 1) &= \frac{e^r}{L + \ell} \left( \int_{\Omega_D} \int_{\Omega_D} k(x, y) dx dy \right) \bar{u}(t) \\ &= \frac{e^r}{L + \ell} \left[ \int_0^L \int_0^L k(x, y) dx dy + \int_0^L \int_{L+D}^{L+D+\ell} k(x, y) dx dy \right. \\ &\quad \left. + \int_{L+D}^{L+D+\ell} \int_0^L k(x, y) dx dy + \int_{L+D}^{L+D+\ell} \int_{L+D}^{L+D+\ell} k(x, y) dx dy \right] \bar{u}(t) \end{aligned} \quad (70)$$

where  $k(x, y) = \frac{1}{2} e^{|x-y|}$ . It is immediate from the Dominated Convergence Theorem that  $\left[ \int_{\Omega_D} \int_{\Omega_D} k(x, y) dx dy \right] \rightarrow \int_0^{L+\ell} \int_0^{L+\ell} k(x, y) dx dy$  as  $D \rightarrow 0$ . Now

$$\int_0^{L+\ell} \int_0^{L+\ell} \frac{1}{2} e^{-|x-y|} dx dy = L + \ell - (1 - e^{-(L+\ell)}),$$

so that (70) predicts growth for all small enough values of  $D$  if and only if

$$e^r \left( 1 - \frac{1 - e^{-(L+\ell)}}{L + \ell} \right) > 1 \quad (71)$$

which holds if  $L + \ell$  is large enough, since  $e^r > 1$ .

Qualitatively, this prediction is compatible with that of the integro-difference formulation in the preceding subsection. On the other hand,

$$\begin{aligned} \int_{\Omega_D} \int_{\Omega_D} \frac{1}{2} e^{-|x-y|} dx dy &\rightarrow \int_0^L \int_0^L \frac{1}{2} e^{-|x-y|} dx dy + \int_0^\ell \int_0^\ell \frac{1}{2} e^{-|x-y|} dx dy \\ &= L + \ell - (1 - e^{-L}) - (1 - e^{-\ell}) \end{aligned}$$

as  $D \rightarrow \infty$ , so that the condition for a prediction of persistence when  $D$  is large is

$$\frac{e^r}{L + \ell} [L + \ell - (1 - e^{-L}) - (1 - e^{-\ell})] \geq 1. \quad (72)$$

**3.2.3. Conclusions from 3.2.2.** In the integro-difference formulation, one obtains a prediction of growth for large values of  $D$  if and only if the model predicts growth for a single patch of length  $L$ . In the average dispersal success formulation, following along the lines of (70), this condition becomes

$$\frac{e^r}{L} [L - (1 - e^{-L})] \geq 1. \quad (73)$$

It is easy to show that

$$\frac{1}{L} [L - (1 - e^{-L})] \geq \frac{1}{L + \ell} [L + \ell - (1 - e^{-L}) - (1 - e^{-\ell})]$$

for  $0 < \ell < L$ , with equality only if  $L = \ell$ . Consequently, if  $0 < \ell < L$ , it is possible for (73) to hold in circumstances when (72) does not. So if  $0 < \ell < L$ , a prediction of growth in the average dispersal success formulation in the case of single favorable patch of length  $L$  does not guarantee that (70) predicts growth for all large values of  $D$ , in contrast to the spatially explicit integro-difference formulation. Of course, having a prediction of growth in (70) for all large values of  $D$  does force (73) to hold. So if  $0 < \ell < L$ , (73) is a necessary but not sufficient condition for a prediction of growth for large values of  $D$ . Only in the special case when  $L = \ell$  are the predictions of the average dispersal success formulation (70) qualitatively compatible with those of the integro-difference formulation (48) for large values of  $D$ .

3.2.4. *Model analysis when the two favorable regions of habitat are viewed as separate patches.* An obvious way in which one might seek to modify (70) so as to match the predictions of (48) qualitatively for both large and small values of  $D$  would be to view  $(0, L)$  and  $(L + D, L + D + \ell)$  as distinct habitat patches. In this case, the average dispersal success formulation becomes

$$\begin{pmatrix} \bar{u}_1 \\ \bar{u}_2 \end{pmatrix}_{t+1} = e^r \begin{pmatrix} p_{11} & p_{12} \\ p_{21} & p_{22} \end{pmatrix} \begin{pmatrix} \bar{u}_1 \\ \bar{u}_2 \end{pmatrix}_t \quad (74)$$

where

$$\begin{aligned} p_{11} &= \frac{1}{L} \int_0^L \int_0^L \frac{1}{2} e^{-|x-y|} dy dx \\ p_{12} &= \frac{1}{L} \int_0^L \int_{L+D}^{L+D+\ell} \frac{1}{2} e^{-|x-y|} dy dx \\ p_{21} &= \frac{1}{\ell} \int_{L+D}^{L+D+\ell} \int_0^L \frac{1}{2} e^{-|x-y|} dy dx \\ p_{22} &= \frac{1}{\ell} \int_{L+D}^{L+D+\ell} \int_{L+D}^{L+D+\ell} \frac{1}{2} e^{-|x-y|} dy dx. \end{aligned}$$

Again  $e^{-|x-y|} \rightarrow 0$  as  $|x-y| \rightarrow \infty$ . Consequently, we have that as  $D \rightarrow \infty$  (74) tends to the decoupled system

$$\begin{pmatrix} \bar{u}_1 \\ \bar{u}_2 \end{pmatrix}_{t+1} = e^r \begin{pmatrix} 1 - \frac{1-e^{-L}}{L} & 0 \\ 0 & 1 - \frac{1-e^{-\ell}}{\ell} \end{pmatrix} \begin{pmatrix} \bar{u}_1 \\ \bar{u}_2 \end{pmatrix}_t. \quad (75)$$

It is not difficult to show that  $1 - \frac{1-e^{-x}}{x}$  is increasing for  $x \in (0, \infty)$ . Consequently, if  $e^r \left(1 - \frac{1-e^{-L}}{L}\right) > 1$  in (75) (which is the condition for a prediction in the case of a single favorable patch of length  $L$  via (71)), (74) predicts growth at the population level for large values of  $D$ , qualitatively consistent with (50). Indeed, if  $\begin{pmatrix} \bar{u}_1 \\ \bar{u}_2 \end{pmatrix}_0 = \begin{pmatrix} u_{10} \\ u_{20} \end{pmatrix}$ , where  $u_{10} > 0$  and  $u_{20} \geq 0$ , and  $c_L = e^r \left(1 - \frac{1-e^{-L}}{L}\right) > 1$ , then  $\begin{pmatrix} \bar{u}_1 \\ \bar{u}_2 \end{pmatrix}_t$  is componentwise positive with  $\bar{u}_{1t} > c_L^t u_{10}$ . If  $c_\ell = e^r \left(1 - \frac{1-e^{-\ell}}{\ell}\right) < 1$ , the larger patch  $(0, L)$  acts as an on-going source of colonists for the smaller patch  $(L + D, L + D + \ell)$ . In particular, if  $\begin{pmatrix} \bar{u}_1 \\ \bar{u}_2 \end{pmatrix}_0 = \begin{pmatrix} 0 \\ 1 \end{pmatrix}$  in (75),  $\bar{u}_{2t} \rightarrow 0$  as  $t \rightarrow \infty$ .

As  $D \rightarrow 0$ , (74) becomes

$$\begin{pmatrix} \bar{u}_1 \\ \bar{u}_2 \end{pmatrix}_{t+1} = e^r \begin{pmatrix} \frac{1}{L} I_1 & \frac{1}{L} I_2 \\ \frac{1}{\ell} I_2 & \frac{1}{\ell} I_3 \end{pmatrix} \begin{pmatrix} \bar{u}_1 \\ \bar{u}_2 \end{pmatrix}_t \quad (76)$$

where  $I_1 = \int_0^L \int_0^L \frac{1}{2} e^{-|x-y|} dy dx$ ,  $I_2 = \int_0^L \int_L^{L+\ell} \frac{1}{2} e^{-|x-y|} dy dx$   
 $= \int_L^{L+\ell} \int_0^L \frac{1}{2} e^{-|x-y|} dy dx$ , and  $I_3 = \int_L^{L+\ell} \int_L^{L+\ell} \frac{1}{2} e^{-|x-y|} dy dx$   
 $= \int_0^\ell \int_0^\ell \frac{1}{2} e^{-|x-y|} dy dx$ . It is not difficult to see that the condition (71) for  
a prediction of persistence in the model (70) in the case of a single favorable patch  
of length  $L + \ell$  can be expressed as

$$\frac{e^r}{L + \ell} (I_1 + 2I_2 + I_3) > 1. \quad (77)$$

Now the eigenvalues of the entrywise positive matrix in (76) are given as the roots  
of the polynomial

$$\lambda^2 - e^r \left[ \frac{I_1}{L} + \frac{I_3}{\ell} \right] \lambda + e^{2r} \left( \frac{I_1 I_3 - I_2^2}{L \ell} \right) = 0.$$

Consequently, the model (74) predicts persistence for small  $D > 0$  when the principal  
eigenvalue of the matrix in (76), namely

$$\lambda^* = \frac{e^r}{2} \left( \frac{I_1}{L} + \frac{I_3}{\ell} + \sqrt{\left( \frac{I_1}{L} - \frac{I_3}{\ell} \right)^2 + \frac{4I_2^2}{L \ell}} \right) > 1. \quad (78)$$

3.2.5. *Conclusions from 3.2.4.* Qualitatively, such a prediction is again compatible  
with that of the spatially explicit integro-difference model (48). Thus, by viewing  
 $(0, L) \cup (L + D, L + D + \ell)$  as two patches, we are able to match the predictions of  
(48) in a qualitative sense for large and small values of  $D$ .

On the other hand, the conditions for a prediction of persistence in (70) and (74)  
may be quantitatively different unless  $L = \ell$ . Indeed, if  $L = \ell$ ,  $I_1 = I_3$  and  $\lambda^*$   
in (78) reduces to  $\frac{e^r}{L + \ell} (I_1 + 2I_2 + I_3)$ . However, if  $\ell < L$ ,  $\frac{I_1}{L} > \frac{I_3}{\ell}$ , and the left  
hand side of (78) may exceed that of (77). This circumstance is equivalent to

$$\frac{1}{2} \sqrt{\left( \frac{I_1}{L} - \frac{I_3}{\ell} \right)^2 + \frac{4I_2^2}{L \ell}} \geq \frac{L - \ell}{2(L + \ell)} \left( \frac{I_1}{L} - \frac{I_3}{\ell} \right) + \frac{2}{L + \ell} I_2. \quad (79)$$

Since  $\frac{I_1}{L} > \frac{I_3}{\ell}$  and  $I_2 > 0$ , (79) holds if and only if

$$\begin{aligned} \frac{1}{4} \left( \frac{I_1}{L} - \frac{I_3}{\ell} \right)^2 + \frac{I_2^2}{L \ell} &\geq \frac{1}{4} \frac{(L - \ell)^2}{(L + \ell)^2} \left( \frac{I_1}{L} - \frac{I_3}{\ell} \right)^2 \\ &+ \frac{2(L - \ell)}{(L + \ell)^2} \left( \frac{I_1}{L} - \frac{I_3}{\ell} \right) I_2 + \frac{4}{(L + \ell)^2} I_2^2. \end{aligned} \quad (80)$$

Since  $1 - \frac{(L - \ell)^2}{(L + \ell)^2} = \frac{4L\ell}{(L + \ell)^2}$ , (80) reduces to

$$\begin{aligned} & \frac{L\ell}{(L+\ell)^2} \left( \frac{I_1}{L} - \frac{I_3}{\ell} \right)^2 - \frac{2(L-\ell)}{(L+\ell)^2} \left( \frac{I_1}{L} - \frac{I_3}{\ell} \right) I_2 \\ & + \left( \frac{1}{L\ell} - \frac{4}{(L+\ell)^2} \right) I_2^2 \geq 0, \end{aligned}$$

• which in turn is equivalent to

$$\left( L\ell \left( \frac{I_1}{L} - \frac{I_3}{\ell} \right) - (L-\ell) I_2 \right)^2 \geq 0. \quad (81)$$

Clearly one has equality in (81) when  $L = \ell$ . Otherwise, equality in (81) is equivalent to

$$\frac{1}{L-\ell} \left( \frac{1-e^{-\ell}}{\ell} - \frac{1-e^{-L}}{L} \right) = \frac{1}{2} \left( \frac{1-e^{-\ell}}{\ell} \right) \left( \frac{1-e^{-L}}{L} \right). \quad (82)$$

The left hand side of (82) tends to  $\frac{1}{L} \left( 1 - \frac{1-e^{-L}}{L} \right)$  as  $\ell \rightarrow 0$  while the right hand side tends to  $\frac{1}{2} \frac{1-e^{-L}}{L}$ . Since  $\left( 1 - \frac{1-e^{-L}}{L} \right) \rightarrow 1$  and  $\frac{1}{2} (1-e^{-L}) \rightarrow \frac{1}{2}$  as  $L \rightarrow \infty$ , the predictions of (70) and (74) are certainly quantitatively different when  $\ell$  is small and  $L$  is large.

*3.2.6. Model analysis and conclusions when the environment is viewed as three patches.* When we think of the overall environment  $(0, L+D+\ell)$  as consisting of three distinct patches  $\Omega_1 = (0, L)$ ,  $\Omega_2 = (L, L+D)$  and  $\Omega_3 = (L+D, L+D+\ell)$ , the average dispersal success approximation takes the form

$$\bar{u}_i(t+1) = \sum_{j=1}^3 e^{r_j} p_{ij} \bar{u}_j(t) \quad (83)$$

$i = 1, 2, 3$ , where  $r_j = r$  for  $j = 1, 3$  and  $r_j = -s$  for  $j = 2$ . In this case, as  $D \rightarrow 0$ , the  $3 \times 3$  matrix  $[A_{ij}] = [e^{r_j} p_{ij}]$  tends to

$$e^r \begin{bmatrix} \frac{I_1}{L} & 0 & \frac{I_2}{L} \\ \frac{1}{2} \int_0^L e^{-|L-y|} dy & 0 & \frac{1}{2} \int_L^{L+\ell} e^{-|L-y|} dy \\ \frac{I_2}{\ell} & 0 & \frac{I_3}{\ell} \end{bmatrix}$$

The eigenvalues of this matrix are 0 and the eigenvalues of

$$e^r \begin{bmatrix} \frac{I_1}{L} & \frac{I_2}{L} \\ \frac{I_2}{\ell} & \frac{I_3}{\ell} \end{bmatrix}.$$

Consequently, the predictions of (83) mirror those of (74) for small  $D > 0$ . As  $D \rightarrow \infty$ , the matrix  $[A_{ij}]$  tends to

$$\begin{bmatrix} e^r \frac{I_1}{L} & \frac{e^{-s}}{2L} (1 - e^{-L}) & 0 \\ 0 & e^{-s} & 0 \\ 0 & \frac{e^{-s}}{2\ell} (1 - e^{-\ell}) & e^r \frac{I_3}{\ell} \end{bmatrix}$$

which effectively decouples so that (83) predicts growth when  $D$  is large when  $e^r \frac{I_1}{L} > 1$ , again as was the case for the two-patch average dispersal success approximation (74).

**4. Conclusions.** In this section we compare and contrast the results of our analysis. Again, the situation we envision is a one-dimensional spatial universe of unlimited extent in which there are two disjoint focal patches of a habitat type that is favorable to some specified species. Neither patch by itself is large enough to sustain the species in question indefinitely, but a single patch of a size equal to the combined sizes of the two focal patches would be sufficient to sustain a population of the given species indefinitely. Our expectation is that if the distance between the two patches is small enough, the species could persist indefinitely in the larger landscape, but that, if the favorable patches are too far apart, the connection between them becomes tenuous as far as the focal species is concerned, and the species goes extinct in the larger landscape. We have examined this thought problem via five different modeling formulations. Two of these modeling frameworks are spatially explicit (reaction-diffusion equations, integro-difference equations with an exponential (Laplace) kernel) while the other three (metapopulation theory, discrete diffusion equations, average dispersal success matrix models) are spatially implicit. Moreover, the discrete diffusion formulation is employed directly as an approximation to the reaction-diffusion model, and likewise the average dispersal success formulation is an approximation to the integro-difference model. So doing gives us the opportunity to examine how closely the predictions of the presumably mathematically more tractable spatially implicit models match those of their spatially explicit counterparts in the context of an intuitively natural thought problem. Specifically, how much do we lose in the precision of prediction by using a simpler formulation?

Our first observation is that the predictions of the two spatially explicit formulations are very much in sync with each other, so that there is a robustness to their predictions. Both predict that the long term suitability of the landscape for the species in question decreases monotonically as the distance between the two favorable patches increases. In particular, in the reaction-diffusion formulation, if the reciprocal of the diffusion rate  $d$  in (10) - (11) exceeds the principal eigenvalue  $\lambda_1$  for (16) - (18) in the case of a landscape with a single favorable patch of size  $L + \ell$ , but is less than the principal eigenvalue for the same problem in the case of a landscape with a single favorable patch of size  $L$  (recall that we assume throughout that  $L \geq \ell$ ), then there is a critical size  $D_{cr}$  of the gap between the two favorable patches so that (10) predicts that the species in question persists indefinitely when the gap size  $D$  is less than  $D_{cr}$  and predicts that the species goes extinct when the gap size  $D$  exceeds  $D_{cr}$ . Analogously, for the integro-difference model (48) the principal eigenvalue  $\lambda_1$  for (50) is strictly decreasing as a function of gap size  $D$ , so that if there is a critical gap size  $D_{cr}$  so that  $\lambda_1(D_{cr}) = 1$ , (48) predicts persistence

when  $D < D_{cr}$  and extinction when  $D > D_{cr}$ . In both cases the power of the mathematical machinery being brought to bear is considerable, and we are able to derive a criterion for persistence versus extinction in the predictions of the models that we can, in principle, test for all values of the relevant parameters.

In considering how well we could match predictions from a discrete-diffusion approximation of the reaction-diffusion model (10) - (11) to the original model, we focused primarily on the five compartment model (28). The state variable in (28) is a five-tuple of nonnegative numbers giving a representative density of the species in question in the two favorable habitat patches and in the matrix habitat between and surrounding them. We found that if we assume that the combined size  $L + \ell$  of the favorable patches is sufficient for a prediction of persistence in the single favorable patch analogue of (28) (i.e., (31)), then (28) predicts persistence when the gap size  $D$  is small, qualitatively consistent with the predictions of (10) - (11). Moreover, if  $L$  is too small to support a prediction of persistence of the species in question in (31), (28) predicts its extinction when the gap size  $D$  is large, again qualitatively consistent with the reaction-diffusion model (10) - (11).

Now if the combined size of the two favorable patches  $L + \ell$  is exactly at the threshold value in (31), we get a prediction of persistence in (28) for small gap sizes  $D$  except in the case when  $L = \ell$ , where we do get a prediction of extinction in (28) for small values of  $D$ . In contrast, the reaction-diffusion model (10) - (11) always predicts extinction in this case, independent of the relative sizes of the two favorable habitat patches. So while the predictions of (28) are in good general qualitative agreement with those of (10) - (11) when the gap size is large or small, the agreement is not perfect when the gap size is small unless the two favorable patches are the same size.

The fact that (28) is a  $5 \times 5$  system of ordinary differential equations limits our ability to give a precise analysis for all intermediate values of the gap size  $D$ , which we were able to do in the reaction-diffusion model (10) - (11). In light of this feature, it is reasonable to consider "cutting down" further to a three component model in which only the average densities of the species in question in the two favorable patches and the gap between them are considered. In this case, the resulting model (45) is readily tractable for all values of  $D$ . However, it predicts persistence when the gap size is small, independent of the size of  $L + \ell$ , which does not comport with the predictions of (10)-(11) when gap sizes are small. (As noted earlier, such findings are in line with the predictions of a reaction-diffusion model on finite domain with a reflecting boundary.) Consequently, we can not reduce the  $5 \times 5$  model (28) in the manner of (45) if we expect to have predictions which are in qualitative agreement with those of (10) - (11) for large and small gap sizes.

In considering the average dispersal success matrix model as a surrogate for the integro-difference model (48), we considered three possibilities. Namely, we first considered only the two favorable habitat patches but viewed them as a single patch (70). Then we again considered only the two favorable habitat patches but viewed them as separate patches (74). Finally, we considered the two favorable patches and the matrix habitat in between them as three patches (83). In the first case, we do get a prediction of persistence when the gap size is small, which is qualitatively consistent with the original integro-difference model (48). However, viewing the favorable habitat as a single patch in this way leads to a more strenuous condition for persistence when gap sizes are large than is the case with (48), unless the two parts of the favorable habitat have the same size. In essence "cutting down" to a

$1 \times 1$  matrix model is too much of a reduction when one has two separated favorable patches.

Viewing the two parts of the favorable habitat as separate patches in (74) (which, of course, seems only natural), we are able to obtain a prediction of persistence in the case of large gap sizes exactly when the larger patch is sufficient in and of itself for the persistence of the species in question, as in (48). Moreover, the predictions of (74) and (48) are qualitatively compatible for small gap sizes. However, the model (74) predicts persistence for small gap sizes when  $L + \ell$  is at the threshold value for the corresponding single patch  $1 \times 1$  matrix model unless  $L = \ell$ . This limitation is the same one we found in using the discrete-diffusion model (28) to approximate the reaction-diffusion model (10) - (11). Going beyond (74) to the three patch model (83) gives the same predictions for large and small gap sizes but does not enhance the information we get from (74). Consequently there is little to be gained from switching from the 2 patch to the 3 patch case when considering the average dispersal success formulation.

Notice that we needed a five dimensional system of ODE's to approximate the predictions of the reaction-diffusion model (10) - (11) with a precision comparable to that we achieve by using a  $2 \times 2$  matrix system to approximate the integro-difference model (48). This feature reflects something of the difference in the way reaction-diffusion formulations and integro-difference formulations represent dispersal. In the discrete-diffusion formulation we need to consider directly what happens in all the areas of unfavorable habitat in order to capture dissipation in a manner that is compatible with a reaction-diffusion formulation. Such is unnecessary in approximating integro-difference models via average dispersal success matrix models.

Finally, while the metapopulation model (3) is not directly a surrogate for either of the spatially explicit models, it is instructive to examine its predictions in the light of those of the other formulations. We are able to get a prediction of persistence when the gap size  $D$  is below a threshold value provided the combined size of the two favorable habitat patches is large enough and the relative sizes of the two patches are somewhat close. When such a prediction is possible, we are able to derive a criterion for persistence versus extinction in the predictions of (3) that we can test for all values of the relevant parameters, just as in the spatially explicit models. Indeed, the criterion in the case of (3) is the simplest of all the formulations we have analyzed. However, the metapopulation approach is limited in its applicability to the problem at hand by its very nature, as the metapopulation framework does not permit the consideration of a single habitat patch. Moreover, having the rate of emigration from a patch be inversely proportional to its size limits how small a secondary patch can be relative to a primary patch, even if the combined size is large enough as in (9). Consequently, while the predictions of discrete-diffusion models and average dispersal success matrix models display some anomalies in precisely mirroring those of their spatially explicit counterparts as gap size approaches zero, the limitation in the case of a metapopulation approach is more fundamental. Nevertheless, it is intriguing that metapopulation models do provide comparable information in this context.

A general conclusion from our analysis is that it is fairly straightforward to construct patch models that capture the qualitative predictions of more sophisticated reaction-diffusion or integro-difference models in simple landscapes. However, some care must be taken in how the patch models are formulated, and precise quantitative agreement between patch models and more realistic models cannot be achieved



in most cases and requires careful tuning of parameters when it is possible. A key point in formulating models that capture the essence of continuum models is to use enough patches to account for all the sources and sinks in the system. For reaction-diffusion models of two patches of favorable habitat in an infinite matrix of unfavorable habitat, the loss of population due to dispersal into hostile regions at  $\pm\infty$  must be built into the corresponding patch model to match the predictions of the reaction-diffusion model qualitatively. One may do so naturally by using five patches, one for each source or sink, but to do so with fewer patches would require ad hoc adjustment of coefficients to account for losses from dispersal out of the patch system. In the case of the average dispersal success approximation to an integro-difference model, to capture the qualitative behavior of the original model, the regions of favorable habitat must be viewed as independent patches, resulting in a two patch model.

Another important conclusion from the analysis is that the situations in which patch models best capture the qualitative behavior of continuum models in simple two-patch landscapes is when the two patches are identical except for location. In both the integro-difference and reaction-diffusion contexts, patch models capture the qualitative features of continuum models more reliably in cases where the patches are the same size. The greatest deviations between the predictions of patch and continuum models arise in cases in which the patches are of different sizes and the combined size of the two patches is at the threshold for supporting a population. In such cases, the question of persistence versus extinction becomes delicate and subtle, and may require sophisticated models for its resolution.

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