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Source: *The American Naturalist*, Vol. 182, No. 1 (July 2013), pp. 42-52

Published by: [The University of Chicago Press](http://www.press.uchicago.edu) for [The American Society of Naturalists](http://www.american-naturalist.org)

Stable URL: <http://www.jstor.org/stable/10.1086/670661>

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How Individual Movement Response to Habitat Edges Affects Population Persistence and Spatial Spread

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Submitted April 4, 2012; Accepted February 5, 2013; Electronically published May 15, 2013

Online enhancements: appendixes.

ABSTRACT: How individual-level movement decisions in response to habitat edges influence population-level patterns of persistence and spread of a species is a major challenge in spatial ecology and conservation biology. Here, we integrate novel insights into edge behavior, based on habitat preference and movement rates, into spatially explicit growth-dispersal models. We demonstrate how crucial ecological quantities (e.g., minimal patch size, spread rate) depend critically on these individual-level decisions. In particular, we find that including edge behavior properly in these models gives qualitatively different and intuitively more reasonable results than those of some previous studies that did not consider this level of detail. Our results highlight the importance of new empirical work on individual movement response to habitat edges.

Keywords: edge behavior, spatial heterogeneity, population dynamics, reaction-diffusion equations.

Introduction

Many empirical and theoretical studies have explored the effects of habitat fragmentation on various species, from plants and insects to birds and mammals (Shigesada et al. 1986; Debinski and Holt 2000; With 2002; Schtickzelle and Baguette 2003; Van Houtan et al. 2007; Dewhurst and Lutscher 2009). A salient feature of fragmented landscapes are edges, defined broadly as interfaces where landscape characteristics change abruptly (Lidicker 1999). Such edges can have several effects on population density and distribution (Ries et al. 2004), often related to individual movement behavior at these landscape features.

Novel experiments and technology provide insights and data on how individual movement characteristics change in response to edges. Schultz and Crone (2001) demonstrated such changes for a prairie butterfly (*Icaricia icarioides fenderi*) within a patch, outside of a patch, and near

edges (see also Crone and Schultz 2008); edge behavior significantly increased residence time in a favorable patch. Ries and Debinski (2001) showed that a habitat specialist (*Speyeria idalia*) and generalist (*Danaus plexippus*) butterfly responded differently to different habitat edges and that the specialist returned more frequently to a favorable patch. Reeve et al. (2008) characterized movement rates of planthoppers (*Prokelisia crocea*) in three different habitat types and determined that individuals easily crossed edges between two types but not into unfavorable habitat. Such behavior is highly species specific; a parasitic wasp (*Anagrus columbi*) of these planthoppers shows behavior that is significantly different from that of its host at the same edges (Reeve and Cronin 2010). Movement of forest songbirds is impeded by gaps in the forest cover, and gap-crossing probability decreases with gap size (Creegan and Osborne 2005; Robertson and Radford 2009). Wolves and other large carnivores bias their movement toward forest edges and linear features, on which they travel farther and faster to increase their predation success (Whittington et al. 2005; McKenzie et al. 2012).

Connecting this wealth of information about individual movement to predictions about population-level outcomes such as extinction, persistence, and spread is a formidable task, and there is currently no coherent framework in place. Cellular automata have been used successfully to tackle some of these questions, most notably about dispersal distances, percolation thresholds, and spatial scales (With 2002). Such models can include detailed assumptions about species and landscapes, and they are easily accessible to direct numerical simulation and visualization. However, very few studies consider behavioral response to habitat edges (e.g., Chapman et al. 2007). Reaction-diffusion equations and their underlying random walk models have been applied successfully to spatial ecology (Cantrell and Cosner 2003), specifically for biological movement (Turchin 1998) and invasions (Andow et al. 1990). Shigesada et al. (1986) first studied persistence and

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invasions in patchy landscapes but did not consider individual behavioral response to habitat edges. Consequently, they arrived at the counterintuitive result that slow movement through unfavorable habitat patches could enhance population persistence, whereas fast movement there could decrease the rate of spread. Ludwig et al. (1979) considered the critical size of a single patch surrounded by less favorable matrix, also not incorporating behavior at habitat edges. Cantrell and Cosner (1999) modeled edge behavior and habitat preference using skew Brownian motion (Walsh 1978), which has the undesirable property that habitat edges can act as sources or sinks of individuals. More recently, Ovaskainen and Cornell (2003) modeled random walks across habitat edges, including habitat preference. Their framework was used to estimate movement parameters (Reeve et al. 2008; Reeve and Cronin 2010) and to determine occupancy times (Ovaskainen 2008).

Here, we jointly generalize the work of Ovaskainen and Cornell (2003)—and earlier Nagylaki (1976)—on edge behavior and integrate the results with classical reaction-diffusion models to assess the effects of edge behavior on population persistence and spread. We introduce our modeling framework in the next section, while giving detailed derivations in appendix A (app. A and B are available online). We reexamine the models by Shigesada et al. (1986) for periodically arranged patches and by Ludwig et al. (1979) for a single patch with behavioral response to edges included. We find that some predictions of both of these seminal models differ substantially when edge behavior is considered. Hence, including edge behavior proves essential to correctly understand population-level patterns. We proceed to address some questions on behavior and patch preference that could not be considered in the existing reaction-diffusion framework. In the discussion, we give biological interpretations and identify future challenges for empirical and theoretical work.

Models and Methods

Growth and Diffusion in Heterogeneous Landscapes

In reaction-diffusion models, individual movement is described by a random walk; reproduction occurs locally on the same timescale (Okubo and Levin 2001; Cantrell and Cosner 2003). The equation for the population density $u(t, x)$ at time t and location x in a homogeneous one-dimensional habitat is

$$\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} + f(u), \quad (1)$$

where D is the diffusion coefficient and f describes net growth. Fisher (1937) studied this equation in genetics; Skellam (1951) applied it to ecology. The population de-

scribed by equation (1) persists in an infinite landscape if $f'(0) > 0$ and, with logistic growth $f(u) = ru(1 - u)$, spreads with speed $c^* = 2(Dr)^{1/2}$ when introduced locally (Weinberger 1982).

Skellam (1951) and Kierstead and Slobodkin (1953) considered a single “good” patch, $[-L/2, L/2]$, surrounded by an inhospitable environment and posed the “minimal patch size problem” of how large a good patch has to be to support a population. The answer depends on movement behavior at the boundary. The worst-case scenario that individuals leave the patch upon reaching the boundary and never return is modeled by “hostile” boundary conditions $u(\pm L/2, t) = 0$. Together with the logistic growth term, this yields the minimal size $L^* = \pi(D/r)^{1/2}$. Conversely, if individuals never cross the boundary the population can persist on a patch of any size; this scenario is modeled by “no-flux” conditions $\partial u/\partial x(\pm L/2, t) = 0$. More realistically, density and flux at the boundary are related by Robin’s boundary conditions (Fagan et al. 1999)

$$\frac{\partial u}{\partial x} + \beta u = 0, \quad (2)$$

which reflect movement behavior at the boundary (Van Kirk and Lewis 1999; Lutscher et al. 2006). For $\beta = 0$ ($\beta \rightarrow \infty$), one retrieves no-flux (hostile) conditions, respectively.

Natural landscapes consist of patches of different quality. Growth conditions vary between patches, and movement behavior changes according to habitat features. Accordingly, in model (1) diffusivity D and parameters in function f are constant within a patch but differ between patches. Choosing logistic growth, the density u_i on patch type i satisfies

$$\frac{\partial u_i}{\partial t} = D_i \frac{\partial^2 u_i}{\partial x^2} + u_i(r_i - \mu_i u_i). \quad (3)$$

Mathematically, we require interface conditions that relate population density and flux between adjacent patches, similar to condition (2) at a boundary. Ecologically, these conditions should reflect movement behavior and patch preferences.

Behavior at Interfaces

Previous authors assumed that population density and flux are continuous across an interface (Ludwig et al. 1979; Shigesada et al. 1986; Cruywagen et al. 1996; Lutscher et al. 2006; Artiles et al. 2008; Vergni et al. 2012). Flux continuity is a natural condition that implies that all individuals who leave one patch enter the adjacent patch; none are introduced or lost at the interface. Continuity of den-

sity may be mathematically reasonable but may (Nagylaki 1976) or may not (Ovaskainen and Cornell 2003) be ecologically correct.

Jointly generalizing the work of these authors, we model individual movement within each patch as a random walk with a given time and space step. Upon reaching the interface between patch 1 and patch 2, say, individuals choose to move to patch i with probability α_i , where $\alpha_1 + \alpha_2 \leq 1$. We can interpret parameters α_i as a measure of habitat preference. After applying the usual parabolic scaling, we find that the flux is continuous at an interface but that the density may be discontinuous. More formally, if u_i and D_i denote the density and diffusion rate in patch i , then the interface conditions read (see app. A, sec. A1, for details)

$$u_1 = ku_2 \text{ and } D_1 \frac{\partial u_1}{\partial x} = D_2 \frac{\partial u_2}{\partial x}. \quad (4)$$

Parameter k measures the discontinuous “jump” in density at the interface. Its value depends on habitat preference and on the particular assumptions about individual movement in either patch. In this work, we shall consider the following three scenarios.

Scenario 1. If individuals move from the interface into patch i at the same rate as they move within patch i , we obtain (Nagylaki 1976)

$$k = 1 \text{ or } u_1 = u_2 \text{ (continuous density)}. \quad (5)$$

This scenario may correspond to an abrupt change in land cover (e.g., dense underbrush versus open grassland) and individuals whose movement rate is strongly affected by these physical differences. It implies that individuals enter patches at a low rate if they move slowly in these patches. Foraging theory, however, suggests that individuals should move slowly in favorable patches and should enter these patches with high probability. Scenario 1 cannot accommodate these characteristics.

Scenario 2. Suppose individuals move from the interface into patch 1 with probability $\alpha_1 = \alpha$ and into patch 2 with probability $\alpha_2 = 1 - \alpha$, independently of the movement probability inside patch i . If the step sizes in different patches may differ but the movement rates may not, then we obtain (Ovaskainen and Cornell 2003)

$$k = \frac{\alpha}{1 - \alpha} \sqrt{\frac{D_2}{D_1}} \text{ (discontinuous density 1)}. \quad (6)$$

Here, an individual chooses a patch according to some features and inside a patch adjusts step sizes to, say, the distribution of host plants or other characteristics. In particular, the individual can choose to move into favorable habitat with high probability and then make small steps there to increase residence time.

Scenario 3. In the same setup as scenario 2, if an individual adjusts the probability of movement inside a patch but keeps the step size constant, then we arrive at

$$k = \frac{\alpha}{1 - \alpha} \frac{D_2}{D_1} \text{ (discontinuous density 2)}, \quad (7)$$

as in Ovaskainen and Cornell (2003). Here, the individual waits longer between steps in good patches than in unfavorable ones but moves by the same distance if it moves at all.

In scenarios 2 and 3, we observe two mechanisms for a discontinuity in density: habitat preference ($\alpha \neq 0.5$) and unequal movement rates ($D_1 \neq D_2$). A preference for one of the two patches should lead to a significantly higher density of individuals in the preferred patch. In fact, $\alpha/(1 - \alpha)$ is an increasing function of α and equals unity when there is no habitat preference ($\alpha = 0.5$). But higher movement rate in one patch also leads to a lower population density near the interface in that patch. As individuals move at a high rate, they move away from the interface and spread out faster, so that the density near the interface declines. Previous authors, mentioned above, did not consider habitat preference but used continuous density conditions at the interface also for different diffusion rates in the two patches. As we explore population patterns resulting from these different interface conditions, the most striking differences between previous results and ours emerge in how the diffusion rates influence persistence and spread.

Results

Persistence Condition

We consider a periodically alternating landscape of favorable (type 1) and unfavorable (type 2) patches of length L_1 and L_2 , respectively (Shigesada et al. 1986). Since persistence conditions emerge at low density, we study the linearized equations. We assume that the growth rate in favorable patches is positive ($r_1 > 0$) and larger than that in unfavorable patches ($r_1 > r_2$). When unfavorable patches are sinks ($r_2 < 0$), we ask for conditions under which the population can still persist at the landscape level, depending on interface behavior. In nondimensional quantities,

$$T = r_1 t, \quad X = \sqrt{\frac{r_1}{D_1}} x, \quad D = \frac{D_2}{D_1},$$

$$r = \frac{r_2}{r_1}, \quad S_i = L_i \sqrt{\frac{r_1}{D_1}},$$

the linear model reads (see app. A, sec. A2)

$$\frac{\partial U_1}{\partial T} = \frac{\partial^2 U_1}{\partial X^2} + U_1 \quad (\text{in favorable patches}), \quad (8)$$

$$\frac{\partial U_2}{\partial T} = D \frac{\partial^2 U_2}{\partial X^2} + r U_2 \quad (\text{in unfavorable patches}). \quad (9)$$

At the interfaces, we impose conditions (4).

Following the analysis in Shigesada et al. (1986), we study the stability of the zero solution and find the persistence boundary as the implicit relationship (note $r < 0$)

$$k \tan\left(\frac{S_1}{2}\right) = \sqrt{-rD} \tanh\left(\sqrt{\frac{-r}{D}} \frac{S_2}{2}\right). \quad (10)$$

We illustrate a few cases of how parameters and interface conditions affect population persistence. The maximum size of unfavorable patches that allows persistence is an increasing function of the growth rate in those patches, all other things being equal (fig. 1A, 1B). This increasing relationship holds for all three interface conditions. When $D > 1$, the maximal length of an unfavorable patch is smallest for $k = 1$ and largest for k as in condition (7) (fig. 1A). When individuals move more slowly in unfa-

vorable habitat, the ordering is reversed (fig. 1B). The minimal size of favorable patches that enables persistence increases with the size of the unfavorable patches (fig. 1C). This relationship also holds for all three interface conditions. The minimum size of favorable patches is smallest for k as in condition (7) and largest for continuous density, provided $D > 1$. When $D < 1$, the situation is again reversed (app. A, sec. A2; fig. A1).

Persistence conditions as a function of diffusivity in unfavorable patches differ significantly among the three interface conditions. For continuous density, the maximum size of unfavorable patches decreases as diffusivity increases. In fact, there is a critical diffusivity below which the population persists for arbitrarily large unfavorable patches (Shigesada et al. 1986). The two other interface conditions predict that the maximum unfavorable patch size increases with diffusivity D , either in a decelerating fashion (interface condition [6]) or even in an accelerating fashion (interface condition [7]; see fig. 1D).

The amount of favorable habitat required for persistence is a decreasing function of preference for favorable patches, since individuals are less likely to leave a favorable patch.

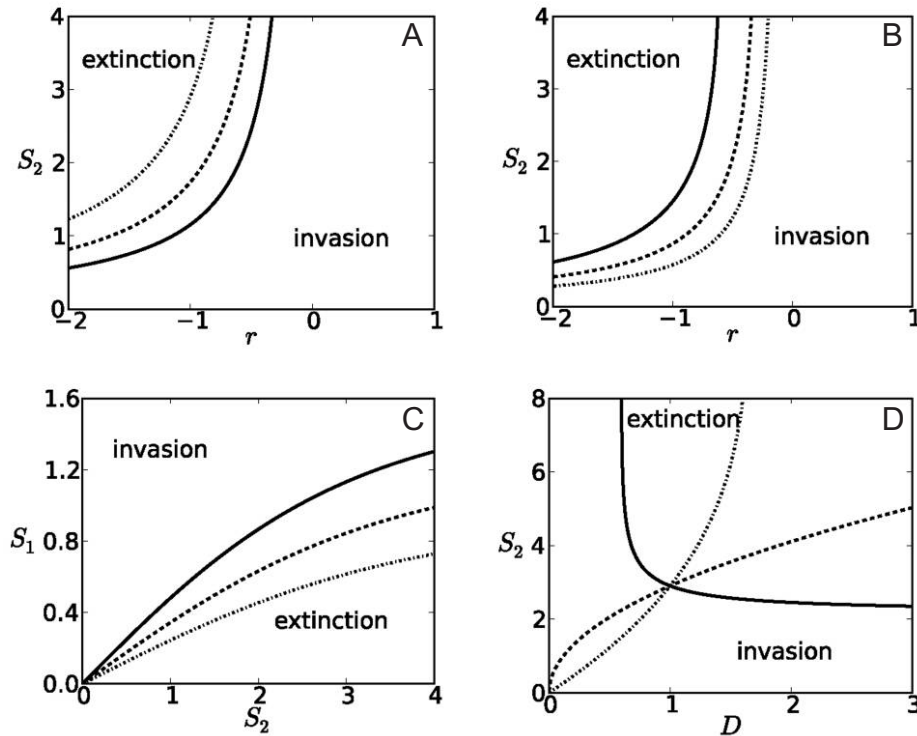


Figure 1: Persistence conditions (10) as a function of unfavorable patch size S_2 and growth rate in an unfavorable patch r (A, B), patch sizes S_1 and S_2 (C), and unfavorable patch size S_2 and diffusivity D (D). The three curves correspond to $k = 1$ (solid curve), k as in condition (6) (dashed curve), and k as in condition (7) (dash-dot curve). Parameters are as follows: A, $D = 2$ and $S_1 = 1$; B, $D = 0.5$ and $S_1 = 1$; C, $D = 2$ and $r = -0.5$; and D, $S_1 = 1$ and $r = -0.5$. We assume that individuals show no habitat preference, so that $\alpha = 0.5$.

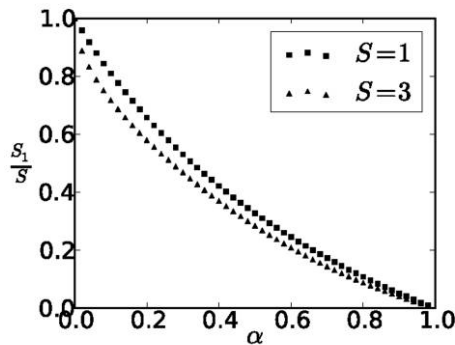


Figure 2: Persistence boundary as a function of habitat preference. The fraction of favorable habitat (S_1/S , where $S = S_1 + S_2$) required for persistence decreases with strength of preference (α). Fixed parameters are $D = 1$ (so that the discontinuous conditions are identical) and $r = -0.5$.

Conversely, the maximum length of unfavorable habitat that allows for persistence increases with preference for good habitat. If preference for favorable habitat is large enough, a population persists even for extremely long unfavorable patches (fig. 2).

Focal Patch Surrounded by Matrix Habitat

As a special case, we consider a single focal patch of good habitat surrounded by a nonlethal matrix habitat (Ludwig et al. 1979). We obtain the minimal size required for persistence on this focal patch by taking the limit $S_2 \rightarrow \infty$ in equation (10) and solving for S_1 as

$$S^* = 2 \arctan \left(\frac{\sqrt{-rD}}{k} \right). \quad (11)$$

For a hostile matrix (i.e., $r \rightarrow -\infty$) one obtains, independently of k , the critical value $S^* = \pi$, which is the threshold for hostile boundary conditions (Skellam 1951).

The qualitative behavior of S^* with respect to parameter r is independent of k ; its dependence on the diffusion rate differs strikingly between the three cases for k . For continuous density, as considered by Ludwig et al. (1979), the critical length increases when diffusivity in the matrix increases; in the discontinuous 2 scenario the critical length decreases as diffusivity in the matrix increases, and in the discontinuous 1 scenario the result is independent of D (see fig. 3). The minimal patch size is a monotonically decreasing function of α , that is, higher preference for the focal patch implies a smaller critical patch size S^* (app. A, sec. A2; fig. A2).

Rate of Spatial Spread

When persistence is guaranteed, a locally introduced population will spread at an asymptotically constant speed, as was demonstrated numerically by Shigesada et al. (1986) and proved analytically by Weinberger (2002) for $k = 1$. The spread rate (c) and its dependence on parameters are arguably the most important quantities in the management of nonnative invasive species (Hastings et al. 2005). We illustrate how this speed depends on interface conditions and patch preference (for detailed calculations, see app. A, sec. A3).

Spread rate increases with growth rate in unfavorable patches (r ; see fig. 4). If $D > 1$, the speed is slowest for continuous density and fastest for discontinuous condition (7); otherwise, the order is reversed (app. A, sec. A3; fig. A4). Points with $c = 0$ correspond to points on the persistence boundary in figure 1A. Curves for different S_2 intersect for some value $r < 1$. Hence, increasing the size of unfavorable patches can increase the spread rate if the movement rate is higher in these patches. Only if unfavorable patches have a sufficiently negative growth rate will increasing S_2 result in slower spread. The spread rate decreases with the size of unfavorable patches; the speed is highest for condition (7) and lowest for $k = 1$ if $D > 1$; the order is reversed if $D < 1$ (app. A, sec. A3; figs. A5, A6).

For both discontinuous interface conditions, spread rate increases with D . When diffusivity in unfavorable patches is small, the population does not spread. As the size of unfavorable patches increases, the threshold diffusivity for population spread also increases (figs. 5B, A3B). Again, zero spread rate corresponds to curves in the persistence plot (fig. 1D). For continuous interface conditions, how-

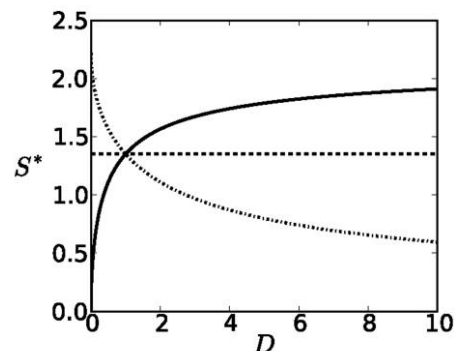


Figure 3: Minimal patch size S^* as a function of diffusivity in the matrix for the continuous density (solid curve), discontinuous 1 (dashed curve), and discontinuous 2 (dash-dot curve) interface conditions. We assume no habitat preference ($\alpha = 0.5$) and $r = -2$.

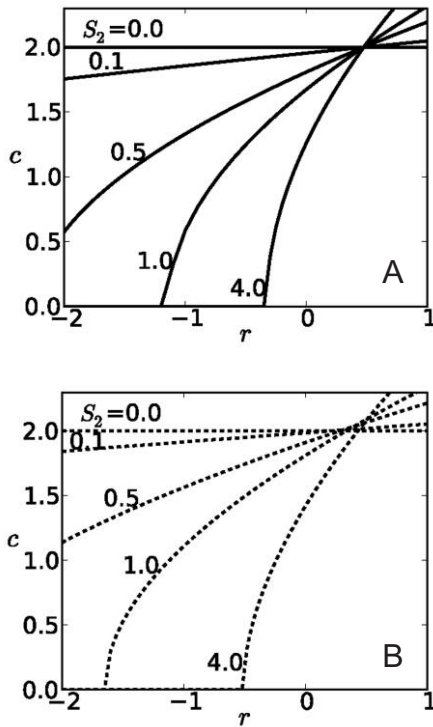


Figure 4: Spread rates as a function of intrinsic growth rate in the unfavorable patch. A corresponds to continuous density at interfaces ($k = 1$), and B corresponds to discontinuous density as in condition (6). Condition (7) is qualitatively similar to B, but speeds are higher (see app. A, sec. A3; fig. A3A). Parameters are $D = 2$ and $\alpha = 0.5$.

ever, the situation is strikingly different (fig. 5A). For any size of unfavorable patches, the spread rate is positive for small D . This finding reflects the result shown in figure 1D, that a population can persist in arbitrarily large unfavorable patches when D is small enough. When S_2 is large enough, the spread rate is a hump-shaped function of D (fig. 5A). Spatial spread halts for large enough D . For comparison, figures 5A, A4A, and A6A and are as in Shigesada et al. (1986).

Spread rate (c) depends on habitat preference (α) via two opposing mechanisms. Higher preference for favorable patches ($\alpha > 0.5$) increases the effective growth rate and thereby the spread rate. High preference for favorable patches also prevents individuals from leaving these patches and moving larger distances in space, which decreases the spread rate. If there is a strong preference for unfavorable patches (α near 0), the population cannot persist or spread, so that $c = 0$ (fig. 6). When the preference for favorable patches increases, the population becomes viable and spreads. The positive effect of α on the spread rate dominates for low to intermediate values of

α ; as preference for favorable patches becomes very strong ($\alpha \approx 1$), negative effects dominate, and c decreases to 0.

In the limit when the period of landscape heterogeneity (L) is small compared with the diffusion coefficients, we derive an explicit approximate expression for the spread rate. We expand the spread rate formula (eq. [A32]), sort by powers of L_1 and L_2 , and obtain the approximation (in dimensional parameters) $c = 2(\langle D \rangle_H \langle r \rangle_A \hat{L}^2)^{1/2}$, where

$$\langle D \rangle_H = \frac{L_1 + L_2/k}{(L_1/D_1) + [(L_2/k)/(D_2/k^2)]},$$

$$\langle r \rangle_A = \frac{r_1 L_1 + r_2 L_2/k}{L_1 + L_2/k}, \tag{12}$$

$$\hat{L} = \frac{L_1 + L_2}{L_1 + L_2/k}$$

are the harmonic mean of the weighted diffusion constant and the arithmetic mean of the growth rate with weights L_1 and L_2/k , as well as the effective period.

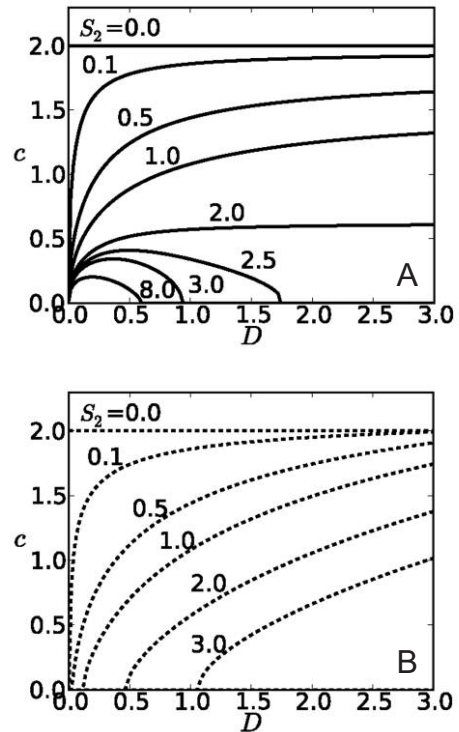


Figure 5: Spread rates as a function of diffusivity in unfavorable patches. A corresponds to continuous density at interfaces ($k = 1$), and B corresponds to discontinuous density as in condition (6). Condition (7) is qualitatively similar to B (see app. A, sec. A3; fig. A3B). Parameters are $r = -0.5$ and $\alpha = 0.5$.

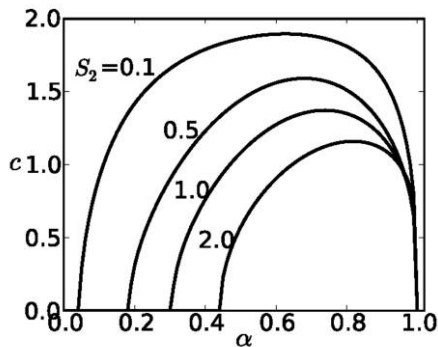


Figure 6: Spread rate as a function of preference for the favorable patches. The minimal value of α that allows spread increases as the size of the unfavorable patch size increases. Parameters are $D = 1$ (so that the two discontinuous conditions are the same) and $r = -0.5$.

Patch Preference Depends on Patch Attributes

We treated parameters as independent, but in reality dependencies and trade-offs exist. Entangling these effects and determining their net outcome provides important future applications of our model. We illustrate the power of our approach with a few examples.

Cantrell and Cosner (1999) considered a core habitat area surrounded by a buffer zone and allowed patch preference to depend on the difference in habitat quality (i.e., α was a function of $r_1 - r_2$; see app. B, sec. B1). This intuitively reasonable assumption leads to the surprising result that a larger core area is needed for persistence if the buffer is of high quality. This effect arises because a high-quality buffer attracts individuals who may subsequently leave the buffer and enter hostile surroundings; a poor-quality buffer, by contrast, creates an aversion to the unfavorable habitat, so that individuals remain in the good habitat and do not enter hostile surroundings. We reproduced these predictions in our model.

Alternatively, preference of a favorable patch may depend on the distance to the next favorable patch. For example, certain bird species that prefer wooded areas (e.g., for cover and protection) may cross open areas (and risk predation) if the nearest wooded area is within reasonable distance (in particular, if it is visible) but not when it is far away (Creegan and Osborne 2005; Robertson and Radford 2009). We explored this possibility by setting patch preference in the periodic environment to

$$\alpha(S_2) = \frac{\alpha_0(1 + \delta S_2)}{2\alpha_0 + \delta S_2} \tag{13}$$

with scaling parameter $\delta > 0$ (Cantrell and Cosner 1999). This function has the following desirable properties. With-

out bad patches, there is no preference ($\alpha(0) = 1/2$). Preference for favorable patches increases with the length of bad patches. For large unfavorable patches, preference is $\alpha_0 \in [1/2, 1]$, whereby 1 corresponds to no-flux conditions.

The critical length of favorable patches is a hump-shaped function of the size of bad patches (S_2). The two opposing mechanisms are as follows. An increase in S_2 leads to higher population loss in unfavorable patches and hence requires larger good patches for persistence. An increase in S_2 also decreases the probability of entering unfavorable patches and, hence, decreases mortality and allows for smaller S_1 . At small S_2 the first effect dominates, whereas for larger S_2 the second effect is stronger (fig. 7). For the rate of spatial spread, increasing S_2 increases loss rates and thereby decreases speed. Increasing S_2 also increases α , which, as in figure 6, can increase or decrease speed when varied independently. The combined effect here acts to decrease the rate of spatial spread. However, higher retention in the favorable patches (i.e., larger α_0) gives higher spread rates, everything else being equal (fig. 7).

Finally, we model a simple network of two favorable patches, each too small to sustain a population, joined by

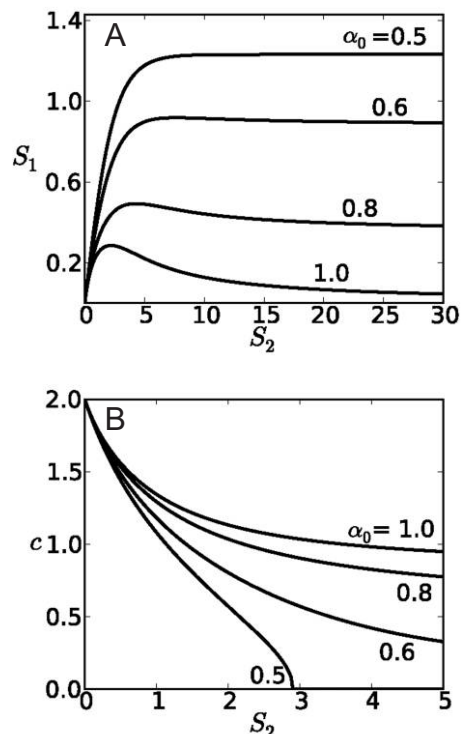


Figure 7: Persistence boundary (A) and invasion speed (B) when gap-crossing depends on gap size. Parameter values are $D = 1$ and $r = -0.5$.

a movement corridor, where net growth is negative (see app. B, sec. B2, for details and figures). All other things being equal, higher corridor mortality requires a shorter corridor for persistence (fig. B2). Individuals could offset high corridor mortality by faster movement. Choosing an appropriate increasing function (in dimensional terms, $D_2 = D_2(r_2)$, similar to eq. [13]) enhances persistence for discontinuous but not for continuous interface conditions. If instead patch preference increases with mortality (i.e., $\alpha = \alpha(r_2)$), two effects can occur. If maximal preference for favorable patches stays below a certain threshold, there is still a maximal distance between the two patches for persistence. If maximal preference is above the threshold, the population can persist even if the patches are very far apart (fig. B3). Preference for the good patch becomes so strong that few individuals leave. When individuals increase patch preference and movement rate in response to decreasing corridor quality, the combined effect increases population persistence even more (fig. B4).

Discussion

As a result of natural disturbances and human activities, landscapes increasingly consist of patches with different characteristics and suitability for different species. Whether a species persists or invades in such a landscape depends on how individuals move in these patches and how they respond to interfaces between different habitat types. A wealth of data is available on movement behavior in different habitat types (Ries and Debinski 2001; Schultz and Crone 2001; Whittington et al. 2005; Reeve et al. 2008), and there is a long history of studying habitat selection and patch preference of animals (Rosenzweig 1981; Brown 1988; Fryxell 2008; Beyer et al. 2010). Yet there was no modeling framework in place to combine this small-scale information and use it to predict population-scale patterns. Here, we extend the applicability of reaction-diffusion models to patchy landscapes by deriving appropriate interface conditions and thereby provide such a theoretical framework. We reanalyze several classical models in ecology and demonstrate how crucially important the correct implementation of interface behavior is to predicting population persistence and spread.

Our derivation of interface conditions generalizes the work by Ovaskainen and Cornell (2003), and it includes the conditions of Nagylaki (1976) as a special case. Hence, we can compare the resulting differences on a mechanistic basis. Specifically, in the absence of habitat preference, the rate of moving into a patch is $1/2$ for the discontinuous conditions, whereas it equals the movement rate in that patch for continuous conditions. We first discuss the effect of differential movement rates, assuming no patch preference.

Effects of Movement Differentials

When individuals move faster in unfavorable habitat ($D > 1$), a population persists under considerably weaker conditions than those found by previous authors (figs. 1A, 1D, 3) and spreads faster through a heterogeneous landscape (figs. 4, A5), at least when unfavorable patches are sinks. When individuals move faster in favorable patches, these findings are reversed. The mechanism behind these results is that under continuous conditions individuals move into unfavorable habitat with a higher probability when $D > 1$ and with a lower probability when $D < 1$. This correlation between movement into and within a patch contradicts foraging theory, which suggests that individuals should move fast within but rarely into unfavorable patches. For example, if forest habitat is disrupted by highway, individuals should enter the highway at a low rate but once there move fairly quickly—a scenario that the continuous conditions cannot accommodate.

Empirically, individuals may move faster in unfavorable patches, trying to reach a favorable patch (Chapman et al. 2007; Reeve et al. 2008). Yet they may move more slowly because of physical obstructions or energy requirements. It is unclear which net effect would emerge (Hastings et al. 2005). We show that whether individuals move faster or slower in certain patches critically affects population patterns and needs to be considered carefully. This suggests that classifying patches by quality needs to include growth potential and individual movement ability (see also Fahrig 2007). For example, the growth potential of a species in agricultural and residential development could be similar, but agricultural land may present fewer obstacles to movement.

Two previous counterintuitive results do not appear here. A population cannot invade when unfavorable patches are large by moving slowly through them (fig. 1D), nor will an invasion slow down when movement in bad patches is fast (fig. 5; Shigesada et al. 1986). This difference arises since movement into and within patches was coupled in previous studies but not in ours. Persistence is ensured by entering bad patches at a low rate, not by moving slowly there. An invasion slows because of frequent movement into bad patches, not because of fast movement there.

Finally, when individuals move faster in less favorable habitat with $r > 0$, increasing the size of less favorable habitat may unexpectedly speed up an invasion (fig. 4). Hence, barrier zones (Sharov and Liebhold 1998) are effective to control invasions only if growth potential is sufficiently low there; otherwise, an invasion may move faster.

These results provide strong theoretical evidence for the importance of including detailed movement behavior at interfaces in population models. Empirical evidence comes

from fitting harvesting data for marine protected areas (Langebrake et al. 2012). Different ecological situations will require different conditions, and we hope that our results will spark empirical work to test different scenarios. For example, one could impose a particular step size by varying spacing between host plants (Turchin 1998, p. 79) while keeping the overall density constant. Alternatively, one could impose temporal movement restrictions to vary movement rates while keeping the spacing of host plants constant.

Effects of Patch Preference

Patch preference (α) introduces into reaction-diffusion models behavioral details that could not be included previously (but see Cantrell and Cosner 1999). Individuals preferentially choose patches for such reasons as higher resource quality or abundance (Brown 1988; Fryxell 2008) and lower predation risk (Brown 1988; Verdolin 2006). Qualitatively, patch preference affects persistence and spread in a relatively predictable way, but our model provides quantitative and sensitivity results. Minimal patch size decreases as preference for the patch increases, and sensitivity to changes in α is greatest when α is either 0 or 1 (fig. A2). In a patchy landscape, a population can tolerate large bad patches if individuals have a strong-enough preference for favorable patches (fig. 2). The rate of spread is maximized at intermediate values of patch preference (fig. 6).

Patch preference helps understand the less intuitive results about differential movement from the expressions for jump size k in conditions (6) and (7). Faster movement in bad patches (higher D) and higher preference for good patches (higher α) both increase k . Hence, faster movement in unfavorable patches has an effect similar to that of higher preference for favorable patches. This observation intuitively explains some results on differential movement, but we caution against scaling motility and preference into a single parameter, since motility also affects population flux at an interface, whereas preference, at least in our formulation, does not.

How General Are These Results?

Cantrell and Cosner (1999) modeled habitat preference via “skew Brownian motion” (Walsh 1978), where habitat preference appears in the flux conditions at an interface. They studied persistence conditions for a species living in a protected core area surrounded by a buffer zone and found that a suitable buffer zone can reduce the required size of the core habitat. We implemented the same scenario with our interface conditions (see app. B, sec. B1, for details). The persistence conditions for our model differ from the ones found by Cantrell and Cosner (1999) only

by a factor of D or $D^{1/2}$, depending on k . Hence, the results with respect to α are robust across model implementations, and we conjecture that there is some deeper mathematical connection between the two approaches than first meets the eye. In particular, the derivation of skew Brownian motion might depend on using Fickian flux or biological diffusion in reaction-diffusion models (Turchin 1998; Glick et al. 2011).

More previous works on dynamics in patchy landscapes should be reexamined in the light of our findings. Conditions for invasion and coexistence between two competing microbes as derived by Cruywagen et al. (1996) will change, as will the results on persistence and invasion in advective environments (Lutscher et al. 2006; Vergni et al. 2012).

Our model is limited to a single spatial dimension and to local movement without temporal variation. Ovaskainen and Cornell (2003) also derive interface conditions in higher dimensions. For long-distance dispersal, one needs to start from an individual-level implementation of the mechanism, just as we did here. In our model, patch preference acts locally only at the interface. Kawasaki et al. (2012) modeled patch preference as attraction from greater distances. Some of their results are similar to ours (e.g., the hump-shaped dependence of c on α), but their model did not include differential movement.

Extensions

Ecologists gather a wealth of small-scale data on movement near interfaces and struggle to explain observations of population densities across edges (Ehrlich 1997; Lidicker 1999). Ries et al. (2004) present a qualitative model for mechanisms leading to positive, neutral, or negative edge effects. We suggest a mechanistic model that incorporates essential information about interface behavior, which was previously impossible in reaction-diffusion equations. We provide a detailed analysis of linear, low-density aspects. The one-dimensional setup could also be applied to corridor design (Andreassen et al. 1996). In the future, we will study nonlinear aspects, such as steady state distributions, and their profile across habitat edges. Some of these questions were already addressed when studying clines in genetics, at least for the continuous case (Nagylaki 1976; Slatkin 1973). We can study the effect of patch preference or differential movement on marginal population dynamics, thereby extending the work of Antonovics et al. (2006), who did not include these factors. Similarly, we suggest reexamining, with appropriate interface conditions, the work of Fagan et al. (2009) on how an Allee effect, together with critical patch size and gap-crossing ability, generates geographic range limits. Finally, we speculate that for interacting species, habitat preference could depend on a competitor or a predator. It will be partic-

ularly interesting to see how the results of Strohm and Tyson (2009) on the existence of limit cycles between predator and prey in fragmented habitats depend on the implementation of interface conditions. Ultimately, a full mechanistic understanding of the wealth of edge effects classified by Ries et al. (2004) will require integration of information across spatial and temporal scales. We suggest that this work is one crucial piece in that great puzzle.

Acknowledgments

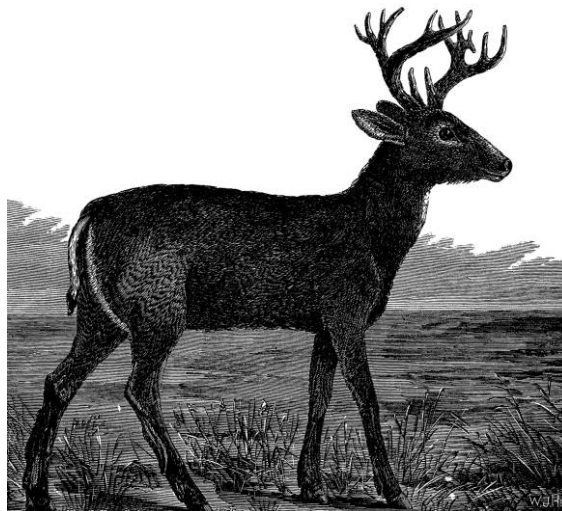
We are grateful for inspiring discussions with C. Cobbold, M. Lewis, J. Musgrave, and O. Ovaskainen. We thank B. Fagan and two anonymous reviewers for valuable feedback. G.A.M. was supported by a grant from Foreign Affairs and International Trade Canada under the Emerging Leaders of the Americas program. F.L. is supported by a Discovery Grant from the Natural Sciences and Engineering Research Council of Canada.

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Associate Editor: Sean H. Rice
Editor: Troy Day



“The Mule Deer ... was first mentioned by Lewis and Clark in the report of their journey up the Missouri River. They gave it the name of Mule Deer on account of the length of its ears; the length of the ear, however, varies with individuals. ... This deer is found from the north of New Mexico to the Saskatchewan, and from the Missouri to the Cascade Mountains.” From “The Mule Deer” by W. J. Hays (*American Naturalist*, 1869, 3:180–181).