VOL. 153, NO. 2 THE AMERICAN NATURALIST FEBRUARY 1999

How Habitat Edges Change Species Interactions

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Submitted January 19, 1998; Accepted July 31, 1998

ABSTRACT: Traditionally, ecologists interested in habitat edges have focused on edge-related gradients in patterns of species richness or abiotic variables. Here, however, we take a different perspective, attempting to synthesize recent empirical results concerning the effects of habitat edges on population dynamics with contemporary theoretical developments to outline the ways in which species interactions, and the dynamics of the communities in which they are embedded, can be changed by habitat edges. We find a striking convergence between empirical notions of a patch's core area and analytical results from partial differential equation models. A review of both empirical and theoretical studies suggests four general classes of mechanisms through which habitat edges can have similar impacts on dissimilar types of species interactions. Specifically, we focus on edges' roles as dispersal barriers or filters, edges' influences on mortality, edges' involvement in spatial subsidies (in which dispersers' intrapatch impacts are maintained by their activities in other habitats), and edges' roles as generators of novel interactions. For each class of edge-mediated effects, we provide examples of how one can use spatial modeling to address the relevant questions on these topics, which together form a key link between community dynamics and landscape structure.

Keywords: community dynamics, edge effects, habitat fragmentation, landscape structure, partial differential equations.

Ecological edges often are treated as little more than ecological curiosities. Indeed, throughout much of ecology's history, scientists have gone to great lengths to conduct research in homogeneous habitats devoid of edges and similar complicating factors. And when ecological aspects of edges have been studied, research typically has emphasized patterns of increased species richness at habitat edges (the original "edge effects"; Leopold 1933; Odum 1971; Kunin 1998) and analyses of vegetational transitions near edges (Wales 1972); that is, researchers studied the ecology of the edges themselves. More recent studies detailing extensive abiotic edge effects (e.g., Kapos 1989; Chen et al. 1995) and linking them to specific population and community impacts (e.g., Saunders et al. 1991; Aizen and Feinsinger 1994) have demonstrated numerous cases in which habitat edges influenced ecological phenomena, ranging from biogeochemical nutrient transport (Kitchell et al. 1979) to the outcome of species interactions (Kareiva 1987; Roland 1993). Such studies demonstrate a marked shift in scientists' interests from traditional edge effect patterns to what we term "edge-mediated effects," in which the focus is not on edge-related patterns themselves but, rather, on the mechanisms through which edges alter ecological processes.

Increasing recognition of the importance of edges has led many researchers (e.g., Bierregaard et al. 1992; Dale et al. 1994; Malcolm 1994) to call for studies of the functional links between habitat edges and community dynamics. A common theme is the critical need to understand the processes through which habitat edges make an impact on species' dispersal and community composition in fragmented versus homogeneous landscapes. At a broader level, researchers have argued that increased research on edge-mediated effects may advance our understanding of some of ecology's major questions, including the scaling of spatial processes (Wiens et al. 1985; Gosz 1993; Wilson 1996), the limitations of island-biogeography theory for terrestrial systems (Janzen 1983, 1986; Boecklen and Gotelli 1984; Doak and Mills 1994), and species-area relationships (Lovejoy et al. 1989; Bierregaard et al. 1992).

Understanding the functional roles of edges is increasingly important because human activities are rapidly influencing the extent (e.g., Groom and Schumaker 1990)

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Am. Nat. 1999. Vol. 153, pp. 165–182.

and type (e.g., Yahner 1988) of edges found on earth. Altered patterns of "edginess" in ecological landscapes seem inevitable because edge creation, destruction, and modification are concomitant features of such increasingly prevalent human activities as habitat fragmentation, centrally organized agriculture (Dempster and Coaker 1974; Ryszkowski et al. 1993), river channelization (Naiman et al. 1988), chemical drift (Landsberg et al. 1990), and selective resource extraction (Suzan et al. 1997).

Our purpose in this article is to synthesize diverse knowledge regarding the impacts of habitat edges on species interactions and community dynamics. To this end, we present a unified mechanistic approach to analytical modeling of edge-mediated effects based on partial differential equations, and we examine the implications of that mathematical approach with respect to four major classes of edge-mediated effects. (Unfortunately, we lack sufficient space to solve such equations here; instead, we concentrate on showing how they can be used to investigate edge-mediated dynamics.) We begin by providing a terminological and conceptual overview of the similarities and differences between ecologists' and mathematicians' views of edges and edge-mediated dynamics, leading to a striking convergence of mathematics and biology involving the concept of a patch's "core area." Drawing on a suite of mathematical and biological examples, we then explore in depth the four general categories of mechanisms through which ecological edges can fundamentally alter species interactions.

Some Comments on Terminology and Approaches

An "edge" is an ecological feature that is hard to define verbally but often is immediately recognizable to observers in the field. Edges are sometimes identifiable as the boundaries separating regions featuring different species of sessile organisms (e.g., mature trees vs. early successional species in fragmented forests; mussel beds vs. algal mats in the intertidal). Such boundaries need not entail sharp, stepwise switches in cover type; gentle gradient-like transitions also can be ecologically important edges. At larger scales, broad ecotones featuring habitats intermediate to, yet distinct from, surrounding regions can function as edges. However, not all species perceive edges visually the way humans do. For example, edgelike changes in soil chemical content (Landsberg 1988), humidity (Kapos 1989), or noise levels (Ferris 1979) can influence species' responses just as visible edges do. Clearly, an edge separating two adjacent habitat types can feature many complementary components that trigger different responses among species.

We use the term "patch" to describe a focal unit of a landscape that is set off from surrounding habitats by an ecologically meaningful edge. Similarly, we make frequent use of the term "matrix" to describe the region surrounding a focal patch. While we recognize that these terms oversimplify the character of most ecological landscapes (see, e.g., Schonewald-Cox and Bayless 1986), we hope our consistent use of these terms will emphasize the mechanistic commonalities that exist among a diverse assortment of edge-mediated effects.

From a mathematical perspective, much of the existing theory related to the dynamical implications of ecological edges uses a framework of partial differential equations (PDEs). Holmes et al. (1994) give an excellent overview of PDEs in ecology in a treatment that helps make central concepts of this body of theory accessible to a broad range of ecologists. More detailed treatments are provided in Murray (1993) and Okubo (1980). In addition to trying to maintain connections to a large body of existing work, we emphasize PDE formulations in this article for two reasons. First, PDEs provide a simple, consistent way of summarizing results and elucidating generalities concerning the interactions between habitat geometry and species interactions (Holmes et al. 1994). Second, as we discuss later, an important and general connection exists between conclusions from PDE theory and the "core area" concept of empirical ecologists. We also hope that our emphasis on a PDE framework in the context of edge-mediated effects will highlight several new areas of research that deserve theoreticians' attention.

The PDEs most often used in ecology are reaction-diffusion equations, which take the general form

$$\frac{\partial u_i}{\partial t} = \nabla \cdot D_i(\vec{x})\nabla u_i + \mathrm{f}(\vec{x},\ \vec{u}) \quad \text{in the habitat patch } \Omega, \tag{1a}$$

$$\alpha_i u_i + \beta_i \frac{\partial u_i}{\partial \boldsymbol{\eta}} = g(u_i) \quad \text{on the edge of } \Omega, \tag{1b}$$

where u_i is the population density of species i, D_i is its rate of diffusive movement, $\vec{x}$ is a location in one or more spatial dimensions, ∇ is the gradient operator (quantifying the rate of change in density in all spatial dimensions), α_i and β_i are, respectively, coefficients modifying species i's density and rate of change at the patch edge, and $\boldsymbol{\eta}$ is an outward unit normal vector along the patch edge (used to relate the orientation of the edge to the direction of dispersal). Note that equation (1a) governs the dynamics inside the patch, while equation (1b) determines what happens at the patch edge (i.e., eq. [1b] specifies the "boundary conditions" of the system, a concept that we treat more thoroughly in the next section).

Theoreticians then modify equations (1) to create specific models of population dynamics and boundary behavior. For example, one can construct the function $f(\vec{x}, \vec{u})$ to incorporate terms for a species' mortality and reproduction, alternative movement dynamics, and interactions with other species, among other considerations. Usually $D_i(\vec{x})$ is a constant, so that $g(u_i) = 0$ corresponds to a fixed ratio of density to flux at the patch boundary, thus characterizing a passive boundary. If $\beta_i = 0$ and $g(u_i)$ is a constant, then equation (1b) describes a constant density on the boundary, whereas if $D_i(\vec{x})$ is a constant, $\alpha_i = 0$, and $g(u_i)$ is a constant, then equation (1b) describes a constant flux across the boundary. In more complicated investigations, the coefficients of equations (1) may be dependent on time, density, or other factors. In addition, although not usually written out, an equation for each species' dynamics in the matrix habitat outside the habitat patch also plays a critical role in models like equations (1). Such exterior equations, which usually take the form of a linear reaction-diffusion equation with a constant death rate, would figure into equations (1) through a "matching condition" that ensures densities and fluxes of both species on both sides of the edge matchup (see Ludwig et al. 1979).

Mathematical and Ecological Perspectives on Patch Edges

Before proceeding, we find it helpful to compare and contrast the ways in which mathematicians and ecologists view patch edges. Such a cross-disciplinary overview provides the common footing necessary for further syntheses regarding edge-mediated effects.

Regardless of the particular equations involved, mathematical analyses of ecological dynamics inside finite patches require information on the behavior of the system's components at the patch edges. Sharp edges and broader edges or ecotones require slightly different mathematical treatments. In the case of a sharp edge, its effect can be described by stipulating movement and mortality on the edge through the boundary conditions given in equation (1b). In the case of broad edges or ecotones, boundary conditions (per se) should be stipulated along the exterior boundary of the ecotone, with the edge between the ecotone and core habitat viewed as an "internal interface" (e.g., Cantrell and Cosner 1993). Internal interfaces often can be described by spatial changes in the coefficients of equation (1a), although complex behavior at such an interface may require more sophisticated modeling.

Mathematicians identify three general classes of boundary conditions suitable for describing sharp ecological edges: reflecting, absorbing, and mixed. These categories of boundary conditions have distinct physical interpretations pertinent to ecological edges.

A habitat patch with reflecting (or "Neumann") boundary conditions is one in which emigration does not occur because any organisms (or propagules) encountering the patch edge "bounce off" and move away from the edge. To produce reflecting boundary conditions, one writes equation (1b) with $\alpha = 0$, $\beta > 0$, and $g = 0$. This parameter combination specifies reflecting boundaries such that movement (technically the "flux") of the species across the edge,

$$-D_i(\vec{x})\frac{\partial u_i}{\partial \boldsymbol{\eta}},$$

tends to zero. As an example, edges between old growth forests and clear-cuts are reflecting boundaries for red-backed voles, which shun the clear-cuts because of the absence of the fungal sporocarps on which they feed (Mills 1995). In comparable systems, reflecting boundaries can engender so-called fence effects in which population densities of small mammals increase with decreasing patch size due to a general reluctance to cross edges (Lidicker 1975; Hestbeck 1982).

In the opposite—but equally extreme—case, patches may feature absorbing (or "Dirichlet") boundary conditions. For such edges, the region outside the patch is interpreted as being immediately lethal. To produce absorbing boundary conditions, one writes equation (1b) with $\alpha > 0$, $\beta = 0$, and $g = 0$, forcing species densities, u_i, to tend to zero at the patch edge. Terrestrial-aquatic edges are absorbing boundaries for seeds of plant species incapable of surviving in both habitats, as is the legislative boundary of Yellowstone National Park for bison dispersing into Montana (where they are shot, ostensibly to control the spread of the disease brucellosis; Dobson and Meagher 1996).

Although ecological cases directly comparable to both reflecting and absorbing boundary conditions certainly exist, most real edges represent a fusion and moderation of the two mathematical extremes, corresponding to mixed (or "Robin") boundary conditions. For mixed boundary conditions, one writes equation (1b) with $\alpha > 0$ and $\beta > 0$. In the specific case of $g = 0$, $\alpha = p$ (where $0 \leq p \leq 1$), and $\beta = 1 - p$, one arrives at the PDE boundary condition directly equivalent to the edge permeability concept of Stamps et al. (1987). When $p = 0$, the boundary is impermeable (reflecting), and when $p = 1$, the boundary is completely permeable (i.e., absorbing; all individuals pass through the edge and are lost to the patch).

We can formulate mixed boundary conditions to describe a variety of ecological edges, including cases where the exterior of a patch is only partially hostile, where some individuals cross the patch edge but others do not, and where organisms will cross the edge only at particular times. One can interpret mixed boundary conditions as saying that individuals crossing the patch boundary are not immediately lost from the population and may return or contribute offspring to the patch (see Ludwig et al.'s study [1979] of spruce budworm dynamics for an ecological application of mixed boundary conditions).

Ecological examples of all three types of mixed boundary conditions commonly occur. For example, dispersal of Yellowstone grizzly bears into degraded habitat, which though not immediately lethal does reduce their probability of surviving, exemplifies the consequences of partially hostile patch edges (Doak 1995). Similarly, partially crossable patch edges can influence the spatial dynamics of invasive plants (Hester and Hobbs 1992) and foraging animals (Bider 1968) when only a fraction of the seeds or animals encountering a habitat edge actually pass across it. In the third case, dispersal behavior at patch edges may vary with time over daily, lunar, seasonal, or successional timescales. (Such variation would be reflected in eq. [1b] by time dependence in α, β, and possibly g.) Examples of periodic boundary conditions include risk-averse foraging of mice near field edges as a function of lunar cycles (Bowers and Dooley 1993), seasonal variation in edge permeability induced by crop cultivation practices (Cummings and Vessey 1994) or snowfall (Oehler and Litvaitis 1996), and the water-level-dependent activities of invertebrate grazers in intertidal "browse zones" (e.g., Paine and Levin 1981).

Traditionally, mathematical models assume that patch edges (whether absorbing, reflective, or mixed) are imperceptible to the dispersing organisms. In such cases, dispersing species are often assumed to diffuse across edges (i.e., they passively flow down density gradients; Pacala and Roughgarden 1982). Such dispersal behavior has management implications for resource extraction in matrix habitat surrounding protected patches (e.g., McClanahan and Kaunda-Arara 1996) and for species conservation inside remnant patches (Schonewald-Cox and Bayless 1986; Buechner 1987; Doak 1995). However, to match more closely biological scenarios in which edge detection is believed important, gradients in edge detectability, sensitivity, or responses can be built into more complex models (Cantrell and Cosner 1999; R. Bommarco and W. Fagan, unpublished manuscript).

The Principal Eigenvalue Quantifies Core Habitat

An important connection between edge-related theory and data deals with ecologists' conceptualizations of edge and core regions of a habitat and the importance of the relative extent of such regions to the maintenance of biotic diversity within a patch (fig. 1; Lovejoy et al. 1986, 1989; Naiman et al. 1988; Laurance and Yensen 1991; Bierregaard et al. 1992). For example, Groom and Schumaker (1990) found that gauging the remaining amount of core habitat in remnant old-growth forest fragments on Washington's Olympic Peninsula was far superior to other edge-related indices (such as mean fractal dimension, shape index, or perimeter/area ratio of fragments) as a measure of regional fragmentation. Similarly, in a simulation study, Stamps et al. (1987) found that the fraction of individuals' home ranges in the core of a habitat patch (i.e., the fraction of home ranges isolated from patch edges) was an important determinant of emigration for a territorial species. Using a line integral approach, Malcolm (1994) demonstrated that simple measures like distance to the nearest edge can give a misleading indication of the extent of unaltered core habitat remaining in a patch.

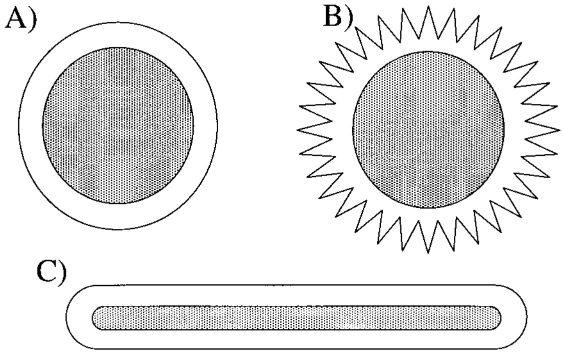

Figure 1: Relationships between geometric patch characteristics from empirical and theoretical perspectives. Shaded areas indicate each hypothetical patch's "core area," while the black line indicates the patch edge. If absorbing (Dirichlet) or mixed (Robin) boundary conditions are imposed on patches *A*, *B*, and *C*, the values for the principal eigenvalue λ_1 (see eqq. [2, 3]) are quite similar and small for patches *A* and *B* but large for patch *C*, reflecting differences in the amount of core habitat. In contrast, the perimeter-to-area ratio is large for patches *B* and *C* but small in *A*. Consequently, the principal eigenvalue λ_1, and hence persistence of the species in the patch, is related to the size of a patch's core habitat rather than its perimeter-to-area ratio. More specifically, for a region of fixed shape, λ_1 scales like $1/\ell^2$, where ℓ is a patch's linear dimension while perimeter-to-area (or surface area–to–volume) ratios scale like $1/\ell$. The relationship is different if completely reflecting (Neumann) boundary conditions are imposed; in that case, $\lambda_1 = 0$ for all patches.

Such recognition of the importance of habitat edges and resulting core areas by ecologists has an important parallel in analytical analyses of theoretical models. In PDE models such as equations (1), a critical factor governing the outcome of both intraspecific and interspecific interactions in a patch frequently is the principal eigenvalue of an eigenvalue problem associated with the PDE model. To give a simple example, consider a single species logistic equation with diffusion:

$$\frac{\partial n}{\partial t} = D\nabla^2 n + rn(1 - n/K)$$

$$\text{in the habitat patch } \Omega, \tag{2a}$$

$$n = 0 \quad \text{on the edge of } \Omega, \tag{2b}$$

where n is the species' population density, K is its carrying capacity, and r and D are its rates of intrinsic growth and diffusion (see Turchin 1998 for a review of methods for calculating D from field data). Whether equations (2) predict persistence or extinction in the patch depends on the size of r/D, a critical ratio that reflects the population's ability to reproduce relative to its mobility. Persistence is predicted if $r/D > \lambda_1$, where $\lambda = \lambda_1$ is the principal eigenvalue of

$$\nabla^2 w + \lambda w = 0 \quad \text{in the habitat patch } \Omega, \tag{3a}$$

$$w = 0 \quad \text{on the edge of } \Omega \tag{3b}$$

(Skellam 1951). In other words, λ_1 is the unique positive number for which equations (3) have an eigenfunction $w > 0$ in Ω.

It is important to note that λ_1 reflects information regarding both the permeability of the edge and the geometry of the patch. As such, λ_1 is a measure of the tendency of organisms to be lost through the patch boundary (see, e.g., Cantrell and Cosner 1994). Although the boundary conditions determine what happens to organisms that reach the patch edge, the organisms' mobility relative to the size of the patch determines what fraction of the total population is actually influenced by the edge. Thus, a good verbal interpretation of the principal eigenvalue is that its reciprocal represents the size of that fraction of a patch that is insulated or otherwise immune from the edge-mediated effects under investigation. Even with hostile boundary conditions, if D is small and/or the domain is large, the boundary exerts relatively little influence over population processes in the patch as a whole. This theoretical result is strikingly similar to the core habitat notion latched onto by ecologists studying landscape fragmentation processes (e.g., Groom and Schumaker 1990) and issues of reserve design (e.g., Janzen 1983) and is quite different from a patch's perimeter-to-area ratio, fractal dimension, and other popular metrics of patch shape (fig. 1). Importantly, r and D can be calculated from field data, and λ_1 can be calculated from patch geometry, so that the condition $r/D > \lambda_1$ governing persistence can be evaluated empirically.

The principal eigenvalue can be used to average spatial effects on a population's intrinsic rate of growth, allowing computation of a quantity (in the case above, $\sigma_1 = r - D\lambda_1$) analogous to the intrinsic rate of population growth observed in more traditional ordinary differential equation models of population dynamics. This averaging across space to yield a growth rate is comparable to the way the principal eigenvalue of a structured population model (e.g., a Leslie matrix) averages reproduction and mortality over classes within a population. In the case of multispecies models, σ_1 for any given species may depend on the presence or absence of other species. If a species has a positive σ_1 when other species are present, then it can increase from low densities and, hence, invade the community. The principle that invasibility implies coexistence permits interpretation of the sign of σ_1 in terms of community structure. This point of view was introduced by Pacala and Roughgarden (1982) in their work on competition in patchy environments and was given mathematical rigor in Cantrell et al. (1993).

Four Principal Classes of Edge-Mediated Effects on Species Interactions

Published literature is surprisingly rich with examples in which processes that create, destroy, modify, or simply maintain habitat edges affect species interactions and influence the composition and dynamics of ecological communities. Rather than delineate our findings according to different types of species interactions (e.g., pollination, competition, predation), we instead search for commonalities in the ways similar edge-mediated effects alter dissimilar species interactions. We suggest that existing empirical and theoretical results can be grouped to reveal four general categories of mechanisms through which ecological edges fundamentally alter species interactions: habitat edges can differentially restrict or facilitate the movement of organisms or propagules among species within a landscape; habitat edges can differentially contribute to the mortality of interacting species; habitat edges can result in "cross-boundary subsidies" (Janzen 1986) in which dispersers' impacts on residents of one patch type are subsidized by their feeding and reproductive activities in another patch; and edges themselves can serve as a unique habitat type, facilitating interactions between species that otherwise would not interact. Which of these classes of edge-mediated effects occurs can depend sensitively on edge characteristics and the species involved. Furthermore, these four principal categories are far from mutually exclusive: particular examples of edge-mediated changes in species interactions may feature components of all four major classes of effects. Nevertheless, it is important to draw distinctions among the different mechanisms because understanding their consequences for the dynamics of ecological communities can require different concepts. Similarly, from conservation and agricultural perspectives, countering (or facilitating) the different mechanisms through which the presence (or absence) of anthropogenic edges alter species interaction regimes can require contrasting management approaches.

Class 1: Edges Can Change Species Interactions by Altering Species' Movement Patterns

The simplest, and perhaps most widespread, class of edge-mediated effects involves habitat edges that facilitate or restrict the dispersal of organisms or their propagules. Such effects are increasingly important because of the tangible connection between landscape modifications like habitat fragmentation and the creation or alteration of habitat edges (Groom and Schumaker 1990; Chen et al. 1995). Consequently, it is not surprising that many researchers have highlighted natural edges (e.g., Abramsky and Van Dyne 1980; Bach 1984; Kareiva 1985), newly induced edges (e.g., Laurance 1991; Aizen and Feinsinger 1994; Dale et al. 1994; Mills 1995), and agricultural edges (e.g., Johnson 1949; Price 1976; Pasek 1988; Landis and Marino 1997) as major sources of disruption for species' dispersal in patchy habitats.

Numerous authors (e.g., Bider 1968; Wegner and Merriam 1979; Wiens et al. 1985; Schonewald-Cox and Bayless 1986) have drawn comparisons between ecological edges and cellular membranes or other biological filters, noting that some edges, like membranes, can be differentially permeable to ecological flows. For a great diversity of taxa, edge permeability is often asymmetric (i.e., immigrants actively cross into patches but are quite hesitant to leave). Such unidirectional edge filtering often results in intense, but short-lived, "supersaturation" of remnant patches as animals flee recently modified matrix habitat for nearby remnants, only to have their densities decline below preisolation levels as resources are exhausted (e.g., Whitcomb et al. 1981). Edge permeability has been examined from several mathematical perspectives, including simulation models (Stamps et al. 1987), integro-difference equations (R. Van Kirk and M. Lewis, unpublished manuscript), and PDEs (Cantrell and Cosner 1999). A prediction from this last study is that edge-sensitive skew Brownian motion (Harrison and Shepp 1981) may result in aggregation along habitat edges, producing spatial patterns similar to those obtained by Kaiser (1983) and Bider (1968) in laboratory and field studies, respectively.

However, edge-mediated disruptions of dispersal have consequences that extend far beyond the single species realm. When habitat edges alter the dispersal patterns of organisms or their propagules so as to change mobile species' encounter frequencies or the dispersion of sessile species, edges can alter the intensity of particular species' interactions and thus make an impact on community dynamics.

The community consequences of dispersal disruptions have long been of interest to those studying plant pollination and seed dispersal in edgy landscapes (e.g., Janzen 1983; Terborgh 1986). By impeding the movements of pollinators, habitat boundaries can restrict pollen flow among plants, dramatically reducing the neighborhood size of reproductive individuals (Aizen and Feinsinger 1994). Edge-mediated movement disruptions also may explain decreased abundance of pollinating euglossine bees in remnant rain forest fragments (Powell and Powell 1987). In general, if edges are prominent landscape features, as they are in severely fragmented habitats, edge-mediated changes in pollinator behavior and density can lead to altered plant composition in forest fragments (Rathcke and Jules 1993).

Edge-altered patterns of seed dispersal may affect plant competitive regimes in similar fashions. When potential germination sites are limiting, among-species differences in cross-edge seed influx may translate into a competitive advantage by influencing the frequency of species self-replacement (Janzen 1983). For example, edge penetration by seeds as a function of "edge closure" (e.g., extensive leaf overlap that reduces edge permeability) appears to have been a key factor underpinning the success and failure of alien plants invading Australian woodlands and shrublands, respectively (Hester and Hobbs 1992). Because competition with invasive species leads to reduced seed production in native annuals, such cross-edge dispersal by seeds from alien plants is an additional threat to biodiversity in already fragmented habitats (Hester and Hobbs 1992). Disturbances associated with edge creation can have profound impacts on edge permeability. In the absence of soil and seed bank disturbances, rapid vegetative growth of primary forest species at the edge may curtail penetration by seeds of matrix-inhabiting species (Williams-Linera 1990), whereas smoke and heat from burning slash at cleared forest edges may result in substantial leaf mortality, offering dispersing propagules easy—but temporary—access to interior areas (Lovejoy et al. 1989).

From a theoretical standpoint, one could use PDEs to explore the impacts of edges on the dispersal of interacting species in several ways. As an example, consider a habitat (the whole of which we will call Ω) that consists of two adjacent patches (called Ω_1 and Ω_2) that are occupied by two competing species. Matrix habitat outside Ω is lethal to both species (i.e., we have absorbing boundary conditions). Furthermore, species 1, but not species 2, recognizes the internal interface separating Ω_1 from Ω_2 and exhibits a movement bias toward Ω_1 (fig. 2). Even if the competitors were otherwise perfectly matched, the species'

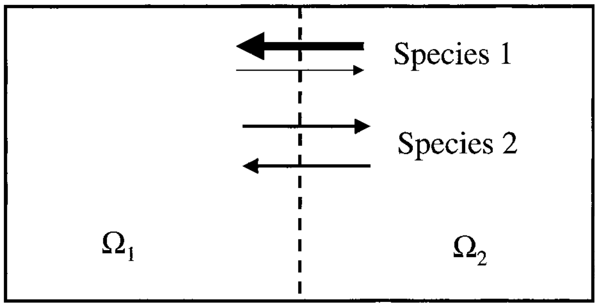

Figure 2: Habitat edges can alter species interactions when only one species detects an edge. In the scenario portrayed above, species 1 exhibits a movement bias away from the internal edge toward patch Ω_1. Over time this movement bias would concentrate the competitive impacts of species 1 on species 2 within patch Ω_1 and could lead to spatial segregation of the two species.

differential sensitivities to the internal edge in this type of model could lead to a spatial segregation of the two competitors between the two patches that would not occur if neither (or both) of the species recognized and reacted to the edge. (Somewhat similar segregative effects are possible even in models featuring only passive diffusive movement when one species is competitively relegated to marginal habitat near the patch boundary; Ali and Cosner 1995.) Mathematically, we could rewrite the preceding example using a pair of diffusive Lotka-Volterra competition equations:

$$\frac{\partial u_1}{\partial t} = D_1\nabla^2 u_1 + r_1\left(1 - \frac{u_1}{K_1} - \frac{a_{12}}{K_1}u_2\right)u_1,$$

$$\frac{\partial u_2}{\partial t} = D_2\nabla^2 u_2 + r_2\left(1 - \frac{u_2}{K_2} - \frac{a_{21}}{K_2}u_1\right)u_2, \quad (4)$$

$$\text{in the habitat patch } \Omega,$$

where u_i is the population density of species i; D_i, r_i, and K_i are, respectively, the diffusion rate, reproductive rate, and carrying capacity of species i; and a_{12} and a_{21} are the competitors' interaction strengths. Absorbing boundary conditions are associated with this model, thus

$$u_i = 0 \quad \text{on the boundary of } \Omega. \quad (5)$$

To account for species 1's movement bias, we also require a matching condition for species 1 at the internal interface such that

$$\alpha\nabla u_1 \text{ (from } \Omega_1 \text{ into } \Omega_2) =$$

$$(1-\alpha)\nabla u_1 \text{ (from } \Omega_2 \text{ into } \Omega_1), \quad (6)$$

where α (which is $\ll 1$) represents the probability that an individual of species 1 crosses from the outer habitat to the inner habitat upon encountering the internal interface. (Thus $\alpha = 1/2$ implies no bias at the internal edge.) Complete analysis of this model seems to be an open problem mathematically.

The same fundamental mechanism—edge-mediated alterations of dispersal patterns—can also disrupt consumer-resource dynamics. For example, edges are strongly reflective for many foraging consumers, acting as a barrier to movement (e.g., Bider 1968). Studies of ladybird beetles foraging in fragmented goldenrod habitats demonstrate how reflective edges can alter consumer-resource interactions: patch edges (manifested as plants with nonoverlapping leaves) alter ladybug turning rates (Kareiva and Perry 1989), delaying aggregation of consumers to incipient prey outbreaks (Kareiva and Odell 1987) and facilitating local explosions of the aphid population (Kareiva 1987). In a similar example, increasing the extent of habitat edges in laboratory microcosms disrupts the movement patterns of both predatory and herbivorous mites, impeding the aggregation of both species and decreasing the predator's functional response in edgier habitats (Kaiser 1983).

In many cases, edges influence consumer-resource dynamics when consumers exhibit risk-averse foraging behavior near edges. For example, during full moon periods, mammalian seed predators inhabiting Virginia old fields face increased mortality risks near patch edges due to heightened predator activity (Bowers and Dooley 1993). At these times of increased risk, the seed predators regularly underuse patch edges at the expense of patch interiors, influencing the spatial distribution of viable seeds in this landscape (Bowers and Dooley 1993). In a comparable system, reduced nut foraging by squirrels at the edges of hickory forests contributes, over the long term, to spatially varying age structure within the hickory population and outward progression of forest edges (Sork 1983). Analogous data on spatial variation in seed predation rates (e.g., Burkey 1993; Osunkoya 1994) and habitat usage (Bider 1968; Kirkland et al. 1985) suggest that edge avoidance by risk-averse seed foragers may be a widespread phenomenon.

On the other hand, intertidal grazers feeding in gaps in mussel beds face greater threats not at patch edges but in patch interiors, where they are exposed to mortality from foraging seabird predators when the tide is out and wave disturbances when the tide is in. The grazers consequently restrict their feeding to the edge of the gap, retreating into the mussel beds for safety (Paine and Levin 1981). Such spatially restricted, risk-averse foraging contributes to the well-known "browse zone" patterns in which the edges of mussel gaps are stripped bare of algae and other biotic substrata but gap interiors sport diverse assemblages of sessile species (Sousa 1984). Similar browse zones occur in terrestrial habitats as well; however, the spatial patterning is somewhat reversed: mammalian herbivores often shelter inside the patch (e.g., under shrubs [Bartholomew 1970], on patches of talus [Huntly 1987]) and forage outside the patch.

In many cases, however, edge-related factors in addition to differential movement play critical roles in determining the nature of species interactions in spatially structured habitats. In such cases simple quantification of different cross-edge movement rates among species gives an incomplete dynamical picture unless such factors as species' demographic rates inside and outside patches are included. As we describe in the following sections, the PDE framework outlined above is robust to these kinds of complications and, furthermore, is well suited to integrating population demographics and species interactions to understand how community dynamics can be affected by habitat edges.

Class 2: Edges Can Change Community Dynamics by Differentially Inducing Species' Mortality

A second major class of edge-mediated changes in species interactions comprises those situations in which edges alter the nature and/or outcome of interspecific interactions through differential influences on species' mortality. Clearly, this category of effects is related to the first, in that individuals must first disperse across the edge before they die outside a patch. But yet the two categories of edge-mediated effects differ in at least one important way: the dynamic consequences of losing an individual from a population via emigration can be less extreme than the consequences of losing an individual through mortality (especially in a multipatch environment). A key theme in this section is that cross-edge movement often entails increased mortality rates. When increased edge-mediated mortality occurs in an unbalanced fashion among species, it can alter the intensity and outcome of species interactions, leading to effects that are in many ways conceptually and mechanistically linked to consumer- and disturbance-mediated coexistence in competitive systems (e.g., Paine 1966; Lubchenco 1978; Connell 1978).

Microclimatic conditions that differ greatly across edges (especially forest–clear-cut edges; Kapos 1989; Chen et al. 1992, 1995) thereby influencing the survival of plant seeds and seedlings (Janzen 1986; Saunders et al. 1991) are one widespread source of edge-mediated differences in species' mortality that can influence plant competitive dynamics. In a landscape comprising remnants of native tropical forests in a sea of harsher modified habitats, edge-related seed mortality may hinder germination of native tree fauna at the expense of environmentally tolerant weedy species, altering successional patterns and making fragmented forest patches even more dissimilar to intact forests (Janzen 1986). Similarly, selective vole predation on seedlings of deciduous trees near forest–old field edges may facilitate conifer invasions into some North American old fields (Ostfeld et al. 1997).

To see the competitive consequences of edge-related mortality more generally, consider a theoretical scenario in which cross-edge dispersal entails a higher risk of mortality for individuals of a competitively superior species than for individuals of a competitively inferior species living in the same patch. If sufficiently strong, such edge-mediated effects could prevent within-patch competitive exclusion of the inferior competitor by the superior one or, in a more extreme case, result in a competitive reversal inside the patch that drives the nominally superior competitor to extinction (Cantrell et al. 1999). The converse is also of ecological interest: greater edge-related mortality for an inferior competitor would likely speed its local extinction.

To explore this issue, we constructed a special boundary condition that allowed us to investigate the consequences of steadily worsening exterior conditions (i.e., matrix habitat degradation) on the patch's competing species using a tunable matrix "hostility" parameter (Cantrell et al. 1999). However, in the present context, this approach speaks more generally to the important role that edge-related mortality can play in competitive dynamics. For example, given a situation in which environmental conditions outside a patch's boundaries favor one competing species over another, the competitors' differential sensitivity to matrix mortality interacts with their rates of crossing the patch edge to determine the outcome of their competitive interaction (fig. 3).

Specifically, we used diffusive Lotka-Volterra competition equations (eqq. [4]) inside the patch, but changed the boundary conditions to

$$\alpha_i \nabla u_i \cdot \eta + \sqrt{s} u_i = 0 \qquad i = 1, 2$$
$$\text{on the boundary of } \Omega, \tag{7}$$

where $\alpha_i = (D_{\text{in}})_i / \sqrt{c_i (D_{\text{out}})_i}$. Here $u_i = u_i(x,t)$ is the population density of species i at position x and time t in the patch Ω, and $(D_{\text{in}})_i$ and $(D_{\text{out}})_i$ are the diffusion rates of species i in the patch and in the matrix, respectively, s is an overarching mortality rate induced by a given level of matrix hostility, and c_i is a proportionality constant scaling the effect of that matrix hostility for species i.

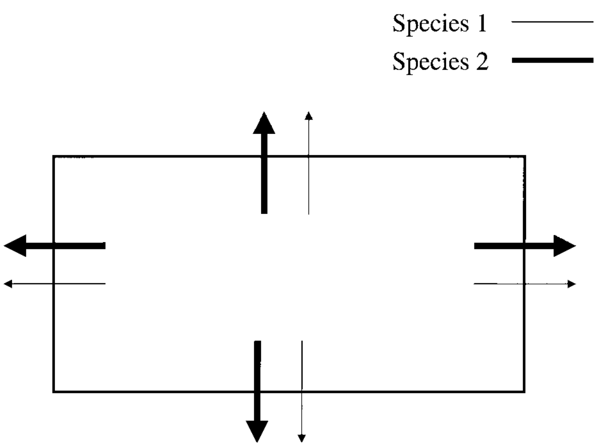

Figure 3: Competitive reversals inside a patch can be mediated by patch edges. The thickness of the arrows represents the impact of edge-related mortality on the two competing species, where mortality can reflect both interspecific differences in dispersal across the edge and interspecific differences in sensitivity to the hostility of the matrix habitat (see, e.g., Cantrell et al. 1999). When faced with sufficient exposure to hostile matrix habitat, an inferior competitor can outcompete a superior one.

Edge-related mortality can play a critical role in consumer-resource interactions as well as competitive ones. Edges' roles as barriers to successful movement are often important features in this context. For example, foragers that hesitate, or are unable, to cross habitat edges and instead travel parallel to them may result in a disproportionate increase in forager activity density near edges, leading to increased consumption in areas immediately near edges (Bider 1968; Gates and Gysel 1972). Conversely, edges that increase mortality of wide-ranging foragers—or at least discourage their entry into patches—may facilitate in-patch population growth of resource species (e.g., birds in road-bounded habitats to which terrestrial predators have reduced access; Pasitschniak-Arts and Messier 1995).

Klein (1989) demonstrates how edge-related mortality along Amazonian forest–clear-cut edges can alter rates of dung and carrion decomposition by edge-sensitive beetles. Rather than being hesitant to cross forest–clear-cut edges, larval and adult beetles may regularly attempt to cross such boundaries, only to die of dessication in the more exposed habitats. The beetles' apparent inability to avoid crossing into areas of increased mortality appears linked to a compositional shift in the carrion-feeding guild: ants become increasingly dominant and carrion beetles relatively less important in small fragments and clear-cut areas where the effects of induced edges are most pronounced (Klein 1989).

Likewise, in fragmented North American forest landscapes, edge-associated changes in abiotic conditions have an impact on outbreaks of forest-defoliating lepidoptera. There, increased edge density (km edge/km^2 landscape) increases the duration of tent caterpillar outbreaks (Roland 1993) by exposing the caterpillars' natural enemy (a nuclear polyhedrosis virus) to increased mortality from UV radiation (Roland and Kaupp 1995), which is much more intense at forest edges than forest interiors. In a similar system, habitat edges that expose spruce budworm larvae to mortality from predators and parasites can limit the spatial spread of outbreaks of the herbivores (Ludwig et al. 1978, 1979).

Class 3: Edges Can Alter Species Interactions through Cross-Boundary Subsidies

A third class of edge-mediated effects includes those situations in which cross-boundary subsidies influence the outcome of species interactions. In this category of effects, cross-boundary subsidies arise as populations of some species are maintained at high levels through growth, reproduction, and/or feeding in other habitats but then disperse across patch edges, depressing or otherwise affecting populations of patch residents. Clearly, such issues are closely related conceptually to source-sink dynamics (Pulliam 1988, 1996) in which some local subpopulations of a species are maintained by an influx of immigrants from more productive habitats. That such cross-edge flows can have consequences for species interactions and community dynamics follows naturally from population-level source-sink concepts. In addition, the dynamics of spatially subsidized competitors, consumers, or parasites and their effects on patch residents are in many ways comparable to the dynamics of apparent competition (Holt and Lawton 1994) or "multichannel" omnivory (Polis and Strong 1996). The mechanistic similarities are especially obvious when the coupling of external resource acquisition with cross-edge movement aggravates consumers' impacts on patch residents in much the same way that feeding on alternative prey species (Holt and Lawton 1994) or tapping into alternative trophic channels (Polis and Strong 1996) facilitates reductions in the populations of focal species. Examples of such dynamics are increasingly common. For example, Müller and Godfray (1997) experimentally demonstrated the linkage between cross-boundary subsidies and apparent competition in an aphid-coccinellid system, while Polis and Hurd (1996) demonstrated how biomass transported across the land-water edge from productive marine environments to relatively unproductive near-shore areas can prop up local densities of terrestrial consumer species, intensifying their impacts on other prey.

We emphasize, however, that cross-boundary subsidies have a broader applicability since spatially segregated resources can enhance populations of competitors and mutualists as well as those of consumers (e.g., Janzen 1983; Abrams and Walters 1996). Consequently, the importance of cross-boundary subsidies to community dynamics in an edgy landscape may be linked more effectively to the relative occurrence of habitat specialists versus habitat generalists, whose populations could be subsidized more readily by cross-boundary activities.

This third class of effects also includes one of the most studied edge-mediated changes in species interactions: the so-called ecological trap hypothesis (Gates and Gysel 1972). In this scenario, nesting passerine birds behaviorally favor the edges of forest patches (because of the dual availability of forest cover and foraging areas), but they do so at the perhaps overwhelming expense of increased mortality from edge-foraging generalist predators and nest parasites (e.g., brown-headed cowbirds). This combination of habitat preference and externally subsidized generalist consumers results in an ecological trap as large fractions of bird populations attempt to reproduce in regions of high mortality (Gates and Gysel 1972).

Numerous researchers have expanded upon this basic theme (e.g., Wilcove 1985; Santos and Telleria 1992; Hanski et al. 1996). Angelstam (1986) suggests that the severity of predation impacts on Swedish forest birds by generalist predators (e.g., corvids, foxes, domestic animals) residing in matrix habitat increases as human activities make the forest patch and its surroundings more and more dissimilar. In remnant Ontario woodlots, Friesen et al. (1995) found that populations of only one group of birds (Neotropical migrants) were sensitive to intrusions by generalist predators from nearby developments, resulting in dramatic shifts in community composition along a gradient of increasing human presence. An important concept stemming from this research is that edge-associated nest predation, which can be quite damaging to bird populations in edge-dominated landscapes (Temple and Cary 1988), is often merely incidental to the edge-foraging consumers: their impacts on bird populations are subsidized by extensive feeding on other species in other habitats (e.g., Pasitschniak-Arts and Messier 1995). Conceptually similar mechanisms, which link spatially subsidized generalist consumers to incidental (but, from an agricultural perspective, critical) impacts on focal species, underlie emerging ideas in biological control using generalist predators (e.g., Murdoch et al. 1985; Settle et al. 1996; Ives and Settle 1997) and polyphagous parasitoids (e.g., Marino and Landis 1996).

Like edge-nesting birds, many species actively seek out and move toward habitat regions that are perceived as being of high quality. However, in edge-dominated landscapes such movement may not always be profitable. Belgacem and Cosner (1995) used PDE models to investigate the consequences of a species' tendency to disperse up gradients in habitat quality inside a habitat patch. They showed that if good-quality habitat was located near a lethal habitat edge, then dispersal up the gradient in habitat quality could involve a net loss to the population.

Cross-boundary subsidies of organisms or their propagules can alter the dynamics of competitive regimes in manners that mirror the effects of subsidies on consumer-resource dynamics. Janzen (1983) described an example in which cross-edge seed influx from weedy, early successional species occupying a buffer zone (akin to a wide edge region) surrounding a remnant forest patch (fig. 4) could prevent reestablishment of forest interior tree species and disrupt the competitive regimes and successional trajectory of the remnant patch. A theoretical treatment of Janzen's case study (Cantrell and Cosner 1993) suggests that a weed species' success in the surrounding matrix often could subsidize the influx of weed seeds into the patch at the expense of competitively dominant resident species. Naturally, the consequences of such subsidies for the competitive success of the weed species in the remnant patch depend on a number of ecologically relevant factors, including the size of core area of the remnant forest patch, the width and harshness of the buffer zone, and the dispersal abilities of the competing species (fig. 4). One startling result from Cantrell and Cosner (1993) was that, if cross-boundary subsidies are severe, buffer zones around ecological reserves, however well intentioned, could sometimes do more harm than good, resulting in the edge-mediated competitive elimination of focal species.

Cantrell and Cosner (1993) arrived at these conclusions using a modified version of the diffusive Lotka-Volterra competition equations given in equations (4). Specifically, they kept equation (5) as the boundary conditions but

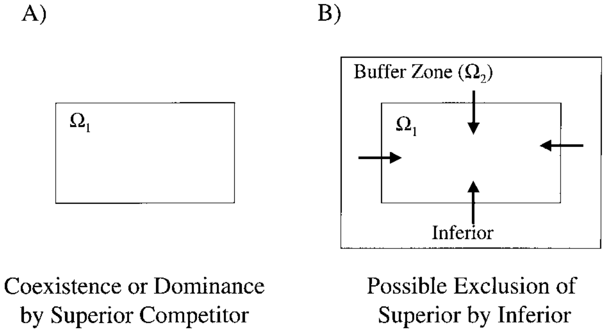

Figure 4: Cross-boundary subsidies can determine the outcome of competitive interactions. *A*, When the patch Ω_1 is isolated from external influences, equations (8) predict coexistence of the two competitors or exclusion of the inferior species by the superior species. In contrast, when the inferior species has a competitive advantage in the outer habitat (*B*), it can outcompete the superior species by building up density in the outer habitat and dispersing into Ω_1.

changed equations (4) so that each species' reproductive rate, carrying capacity, and interaction strengths were functions of spatial position (i.e., the coefficients were constant within the remnant patch and within the buffer zone but differed between those regions). Mathematically, this can be written

$$\frac{\partial u_1}{\partial t} = D_1\nabla^2 u_1 + r_1(x)\left[1 - \frac{u_1}{K_1(x)} - \frac{a_{12}(x)}{K_1(x)}u_2\right]u_1,$$

$$\frac{\partial u_2}{\partial t} = D_2\nabla^2 u_2 + r_2(x)\left[1 - \frac{u_2}{K_2(x)} - \frac{a_{21}(x)}{K_2(x)}u_1\right]u_2. \tag{8}$$

In studies of nest predation, seed dispersal, and similar processes, penetration of a species or altered abiotic conditions into a patch (or the inferred consequences of such penetration) is often quantified simply as a function of distance to the nearest edge (Groom and Schumaker 1990; Laurance and Yensen 1991). However, the utility of this "penetration profile" approach decreases with decreasing patch size as an individual locale comes increasingly under the influence of multiple edges. In particular, as patch size decreases, interactions among effects of multiple edges could result in the elimination of core habitat long before one would expect it to disappear based on measurements of distance to nearest edge alone. A more general approach to dealing with such intrusive edge effects uses line integrals to summarize a site's isolation relative to multiple edges (Malcolm 1994). Resolving the linkages between cross-edge intrusions and their community consequences remains an open issue for ecologists. Meshing empirically determined penetration profiles with dynamical models may offer one feasible approach.

Edge-mediated effects involving cross-boundary subsidies also can occur in the reverse direction, going from the inside out. Temporary emigration and cross-boundary foraging by large mammals in response to density or resource pressures (Janzen 1986; Dobson and Meagher 1996) is a well-known example. Although one might be tempted to view such outwardly directed foraging in the same light as intrusive effects simply by reversing one's definition of "patch" and "matrix," subtle but important mechanistic distinctions often preclude such a straightforward solution. In contrast to intrusive effects that often may involve incidental foraging by a species whose population is otherwise subsidized, cross-boundary foraging from the inside of a patch outward may often focus on access to essential rather than supplementary resources (e.g., survival during drought years; Boone and Keller 1993). Such inside-out foraging can influence the intensity of competitive interactions in surrounding matrix habitat (e.g., Huntly 1987) and can depend upon predation risks faced during foraging activities (Johnston and Naiman 1987).

Finally, in many instances, edge habitats themselves can provide a population subsidy for some species. To the extent that species make differential use of such edge areas, altering the relative availability of edge and core habitats among patches can determine the outcome of species interactions. As a case in point, Pearman (1995), who studied a two-species larval anuran system in microcosms where edge habitat corresponded to enclosure surface area near the air-water interface, found that high edge/interior ratios favored the growth and survivorship of the tadpole species that more effectively fed on periphyton growing on enclosure surfaces.

Class 4: Edges Can Create New Opportunities for Species Interactions

The fourth class of edge-mediated changes in species interactions emphasizes edges' roles as generators of novel species interactions, a function of edges long recognized by researchers (e.g., Leopold 1933; Odum 1971). Landscape ecologists also have been interested in edges' roles as generators of species interactions, in one case focusing on how edge-dependent browsing could influence the successional propagation of forest edges across landscapes (Hardt and Forman 1989). In the conservation literature, attention has focused on the negative impacts of anthropogenic edge creation through the generation of detrimental or otherwise inappropriate species interactions (e.g., Yahner 1988). In Amazonia, Lovejoy et al. (1989) demonstrated that the consequences of edge creation may quickly span multiple trophic levels as new interactions are facilitated. In one example, lush plant growth along newly created edges spawned a burst of insect herbivores that soon attracted insectivorous species, altering the species composition of rain forest fragments relative to contiguous forest (Lovejoy et al. 1986, 1989).

In this fourth class of edge-mediated effects, the influences of habitat edges on the interspecific differences in dispersal once again are critically important. Edges that act as biological barriers (e.g., Wegner and Merriam 1979) may increase animal movement parallel to edges resulting in "travel lanes" (Bider 1968; Kaiser 1983) that generate a disproportionately high frequency of interspecific contacts at edges. For instance, edges that function as travel lanes for generalist predators are key components of the ecological trap hypothesis discussed earlier (Gates and Gysel 1972; Angelstam 1986). Similarly, construction of impermeable fence lines along roads in Banff National Park, Canada, to reduce roadkill has increased ungulate activity densities near highway underpasses where dispersal is possible; wolf attacks on ungulates have increased near these underpasses accordingly (e.g., Woods 1989). In addition, increased activity and contacts in the vicinity of edges may generate an interaction vacuum in other portions of a landscape where species spend disproportionately less time (Bider 1968). (The converse scenario also would be possible in that, if species utterly avoid edges and tend to crowd inward toward patch centers, increased contacts would take place in the patch core while an activity vacuum developed near the patch fringes; see, e.g., Bowers and Dooley 1993.)

The types of novel interactions spawned by habitat edges span the entire ecological gamut. For example, in Australian rain forests, edge generation creates opportunities for interspecific competition among rat species, perhaps leading to the local extirpation of one species (Laurance 1994). Similarly, edge creation in old-growth forests of the Pacific Northwest facilitates otherwise atypical predation of great horned owls on juvenile northern spotted owls (e.g., Lujan et al. 1992). Edge-linked herbivory may be an important driver of the widespread dieback of eucalyptus trees in rural Australia as adult herbivorous insects are crowded into forest fragments even as juvenile habitat (i.e., farmed fields) increases (Lowman and Heatwole 1992). Likewise, in the Russian Arctic, where the perimeter of snow-free patches is a strong predictor of abundance for ptarmigan and passerine birds, the edges of melting snowfields facilitate bird consumption of fresh plant growth and recently emerged insects (Summers and Underhill 1996). Edges also can facilitate novel parasitic interactions. Well-known North American examples include edge-linked brood parasitism of passerine nests by brown-headed cowbirds (Brittingham and Temple 1983; Trail and Baptista 1993) and the transmission of brainworm infections from white-tailed deer, where the effects of infection are relatively benign, to other ungulates such as moose, caribou, and elk, where the infections can be lethal (Anderson 1972; Holmes 1996). Remnant Puerto Rican rain forests feature a similar interaction wherein parasitic botflies are transmitted to forest interior species like the endangered Puerto Rican parrot through contacts with reservoir species at forest-matrix edges (Snyder et al. 1987; Loye and Carroll 1995). Like the edge-mediated effects spawned by cross-boundary subsidies discussed earlier, one could roughly characterize these and similar edge-generated interactions as spatially dependent cases of apparent competition.

As in the previous three types of edge-mediated effects, the generation of novel species interactions by edges can be investigated theoretically in the context of PDEs. As an illustration, consider a domain, Ω, consisting of two major regions, Ω_1 and Ω_2, connected by an edge strip, Ω_e (fig. 5). Regions Ω_1 and Ω_2 are, respectively, the main habitats of two potentially competing species 1 and 2, which do not enter each other's primary habitat but do come in contact with each other in the edge region. Although a full analysis of this problem has not been completed, one interesting approach would be to try to find an expression (in terms of the species' reproductive and diffusion rates, their strengths of interaction, and the relative geometries of Ω_e, Ω_1, and Ω_2) that quantifies the extent of competition species 1 could endure from species 2 in the edge region without forcing species 1 extinct or below some critical density threshold in its principal habitat, Ω_1. That is, one would study the ramifications of interactions in edge habitat for species' dynamics in the rest of the region. The dynamics of the two competing species could then be another variation on equations (4), modeled as follows:

$$
\begin{aligned}
&\frac{\partial u_1}{\partial t} = D_1\nabla^2 u_1 + r_1\left(1 - \frac{u_1}{K_1} - \frac{a_{12}}{K_1}u_2\right)u_1 \\
&\qquad\qquad \text{in } \Omega_1 \text{ and } \Omega_e, \\
&u_1 \equiv 0 \quad \text{in } \Omega_2, \\
&\frac{\partial u_2}{\partial t} = D_2\nabla^2 u_2 + r_2\left(1 - \frac{u_2}{K_2} - \frac{a_{21}}{K_2}u_1\right)u_2 \\
&\qquad\qquad \text{in } \Omega_e \text{ and } \Omega_2, \\
&u_2 \equiv 0 \quad \text{in } \Omega_1,
\end{aligned}
\tag{9}
$$

with boundary conditions

$$\frac{\partial u_1}{\partial \eta} = 0 \quad \text{on the boundary between } \Omega_e \text{ and } \Omega_2, \tag{10a}$$

$$\frac{\partial u_2}{\partial \eta} = 0 \quad \text{on the boundary between } \Omega_e \text{ and } \Omega_1, \tag{10b}$$

$$u_1 = 0 \quad \text{on the boundary between matrix habitat and } (\Omega_e \text{ plus } \Omega_1), \tag{10c}$$

$$u_2 = 0 \quad \text{on the boundary between matrix habitat and } (\Omega_e \text{ plus } \Omega_2). \tag{10d}$$

This multipart boundary condition specifies that species i does not wander into the habitat of species j (eqq. [10a], [10b]) and does not survive outside of its own habitat or the edge (eqq. [10c], [10d]).

Conclusion

Ecologists have long decried the lack of information on the specific mechanisms of species loss in habitat fragments (Lovejoy et al. 1986, 1989) and the implications of such losses for community integrity (Janzen 1983; Rathcke and

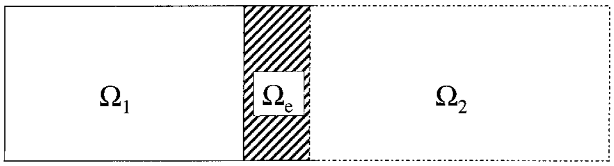

Figure 5: Habitat configuration for the competitive edge contact example involved in equations (9) and (10). Species 1 and 2, respectively, occupy habitats Ω_1 and Ω_2, come in contact with each other in the edge region, Ω_e, but do not enter each other's primary habitat. Even though Ω_e encompasses only a small part of the habitat for both species, their interaction in that region still could alter profoundly their dynamics in their primary habitat.

Jules 1993). Indeed, interest in conservation of particular species in the face of anthropogenic extinction risks has spawned much of the research on edge-mediated effects that we attempted to synthesize here. Yet, the growing awareness of the importance of habitat edges to conservation only hints at the true extent of habitat edges' dynamical significance. Because the edge concept is scalable (e.g., Gosz 1993), extending from the boundaries of individual leaves to continental-scale ecotones among biomes, it touches on many of ecology's major issues. Specifically, by altering the nature of species interactions, habitat edges can influence critical ecological mechanisms, patterns, and dynamics at a variety of spatial scales: edges have the potential to influence everything from species evolution (Smith et al. 1997) to ecosystem function (Klein 1989).

At least two critical themes emerge from this synthesis. The first concerns the importance of among-species differences in overall edge responses for community dynamics. Gaining an understanding of individual species' movements across and along edges provides only a limited view of the ecological consequences of habitat heterogeneity. Combining movement data with information on demographics and species interactions facilitates a more complete interpretation of the overall effects of edges. In such studies, interspecific contrasts in movement and mortality can depend critically on what edge-mediated effects arise. A second emerging theme concerns the roles of spatial supplementation and cross-edge dispersal of competitors, mutualists, and natural enemies as determinants of the outcomes of particular species interactions in habitat patches. Conceptualizing and experimentally documenting the community impacts of such cross-boundary subsidies help link patch dynamics and landscape ecology to food web studies. On a still broader level, edge-mediated dynamics place severe limitations on our application of island-biogeography theory to terrestrial systems (Janzen 1983, 1986; Doak and Mills 1994) and are primary drivers of decreasing species richness with decreasing patch size (Lovejoy et al. 1986, 1989; Bierregaard et al. 1992; see also Cantrell and Cosner 1994 for a PDE-based analysis). In these situations, the influences of edge-mediated effects on the processes of species colonization and extinction, which comprise a conceptual core of both island biogeography and species-area relations (MacArthur and Wilson 1967; Hanski and Gyllenberg 1997), are of central concern.

Prodded, in part, by applied issues in conservation and biological control, ecologists have focused enormous attention in recent years on the effects of habitat fragmentation and patchiness. Much of this work has been couched or conducted in terms of metapopulation dynamics of single species. However, such single-species metapopulation perspectives are often insufficient; they miss or obscure major dynamical attributes of the ecological systems in which they are framed. Because interacting species can differ widely in their responses to the details of habitat structure (e.g., Roland and Taylor 1997), it is becoming increasingly apparent that habitat fragmentation and patchiness have at least as much potential to affect species interactions and communities as they do to affect population dynamics. Similarly, because habitat edges are a principal component of fragmentation and patch alteration, we argue that understanding the impacts of edges provides a key to deciphering how community dynamics change as functions of habitat structure and spatial scale. Consequently, focusing experimental and mathematical efforts on the community impacts of habitat edges will help bring the intense ecological interest in spatial dynamics that is currently devoted to metapopulation and fragmentation studies to bear more directly on the specific mechanisms underlying alterations in community structure and dynamics.

Acknowledgments

We thank R. Bommarco, D. Doak, P. Kareiva, P. Marino, C. McFadden-Wenig, and J. Rango for thoughtful comments that helped us focus our ideas and improved the text. We are indebted to T. Ives and two anonymous reviewers whose comments helped us clarify our objectives and better integrate the mathematics into the text. L. Freidenburg and K. Cottingham provided helpful references. This work was conducted, in part, during W.F.'s participation in the Biological Diversity Working Group supported by the National Center for Ecological Analysis and Synthesis, a center funded by National Science Foundation grant DEB-94-21535, the University of California at Santa Barbara, and the State of California. Start-up funds from Arizona State University provided additional support for W.F. while NSF grant DMS 96-25741 supported research by R.S.C. and C.C.

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Associate Editor: Anthony R. Ives