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ECOLOGICAL RESPONSES TO HABITAT EDGES: Mechanisms, Models, and Variability Explained

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■ **Abstract** Edge effects have been studied for decades because they are a key component to understanding how landscape structure influences habitat quality. However, making sense of the diverse patterns and extensive variability reported in the literature has been difficult because there has been no unifying conceptual framework to guide research. In this review, we identify four fundamental mechanisms that cause edge responses: ecological flows, access to spatially separated resources, resource mapping, and species interactions. We present a conceptual framework that identifies the pathways through which these four mechanisms can influence distributions, ultimately leading to new ecological communities near habitat edges. Next, we examine a predictive model of edge responses and show how it can explain much of the variation reported in the literature. Using this model, we show that, when observed, edge responses are largely predictable and consistent. When edge responses are variable for the same species at the same edge type, observed responses are rarely in opposite directions. We then show how remaining variability may be understood within our conceptual frameworks. Finally, we suggest that, despite all the research in this area, the development of tools to extrapolate edge responses to landscapes has been slow, restricting our ability to use this information for conservation and management.

INTRODUCTION

The edges between habitat patches are often ecologically distinct from patch interiors, and understanding how ecological patterns change near edges is key to understanding landscape-level dynamics such as the impacts of fragmentation. Landscapes are often viewed as patches of habitat and nonhabitat (Figure 1*a*), and thus "edge effects" have often been conceptualized as an ecological change that is due to moving away from the "core" area of a patch and not directly linked to landscape context. In fact, landscapes exist as mosaics of several different patch types (Figure 1*b*), so understanding the ecology of habitat edges requires understanding the complex influences that each different adjacent patch has on a focal patch. As patches become smaller and more irregularly shaped, they become increasingly dominated by edge habitat. Therefore, understanding the ecology of habitat edges is critical both for landscape ecology and for large-scale conservation and management decisions.

Because of their importance and ubiquity, habitat edges are one of the most extensively researched areas in ecology. Most edge studies measure ecological patterns, such as changes in abundance or fitness with respect to the edge. However, the literature covers a wide range of topics, including the factors that maintain or change the position of edges in a landscape (e.g., Arris & Eagleson 1989, Bowman & Fensham 1991, Allen & Breshears 1998, Callaghan et al. 2002, Klasner & Fagre 2002); the identification and measurement of edges within remotely sensed data (e.g., Fortin 1994, Choesin & Boerner 2002, Fagan et al. 2003); the impact of edges on migration through their role in mediating dispersal (e.g., Stamps et al. 1987, Haddad 1999, Ries & Debinski 2001, Schultz & Crone 2001, Schtickzelle & Baguette 2003); and the evolutionary impacts of edges on populations, including speciation (e.g., Smith et al. 1997, Schilthuizen 2000) and the maintenance of hybrid zones (Young 1996). For this review, we focus on ecological responses, particularly species abundance patterns, to the presence of habitat edges. Our goal is to understand the mechanisms that underlie those responses and to place the research into a conceptual framework that helps explain reported patterns and variability. Further, we explore how these patterns may help us understand large-scale dynamics.

Edges are generally defined as boundaries between distinct patch types, so the identification of edges depends on how patches are defined within a landscape. Patch definition can occur at a variety of scales, from patches of different species of plants within a meadow to major biomes within continents (Cadenasso et al. 2003). To limit our scope, we focus on patches of different vegetation or land-use classes (i.e., forests, meadows, scrub, agriculture, urban areas, etc.) within terrestrial landscapes. We refer to any variable that increases near edges as having a positive edge response, a variable that exhibits no pattern as having a neutral response, and a variable that decreases near edges as having a negative edge response (see Figure 2).

The earliest reference to edge-related ecology is attributed to Clements (1907), who introduced the term "ecotone." The influence of these "zones of transition" on wildlife has been noted for decades, with Leopold (1933) using the term "edge effect" to describe the increase in game species in patchy landscapes. Other early accounts of increased diversity near edges (Lay 1938, Johnston 1947) added to the general conception that edges were good for wildlife, and their creation was often recommended in management (Harris 1988, Yahner 1988). The view of edges as

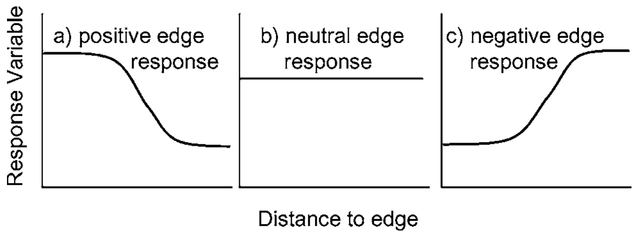


Figure 2 Three classes of ecological edge responses with respect to distance from the closest habitat edge. Responses are generally categorized as (*a*) positive edge responses, where the variable of interest increases near the edge; (*b*) neutral responses, where there is no pattern with respect to the edge; and (*c*) negative responses, where the variable decreases near the edge.

largely beneficial began to change by the late 1970s with the discovery that some birds were experiencing higher rates of nest predation and parasitism near forest edges (Gates & Gysel 1978, Chasko & Gates 1982). This pattern, coupled with increased bird numbers near edges, led many to view forest edges as "ecological traps" (Gates & Gysel 1978) and to suggest that this phenomenon may contribute to the decline of songbirds (Brittingham & Temple 1983, Wilcove 1985). In addition, edges became associated with decreased quality for habitat specialists (Mills 1995, Burke & Nol 1998) and the invasion of exotic species into habitat reserves (Morgan 1998, Honnay et al. 2002). These issues helped form the modern perception of edges, especially anthropogenic edges, as undesirable landscape features (Harris 1988, Saunders et al. 1991).

The past two decades have seen a flood of edge research on a wide range of organisms (Table 1) at an increasingly diverse number of edge types. In addition, a growing focus on mechanisms that underlie edge effects (Murcia 1995, McCollin 1998, Fagan et al. 1999, Cadenasso et al. 2003) has led to many empirical investigations of these mechanisms (e.g., Kingston & Morris 2000, Fletcher & Koford 2003, Kristan et al. 2003). However, highly variable response patterns (Murcia 1995, Villard 1998, Sisk & Battin 2002) create the impression that edges are associated with idiosyncratic responses to disparate ecological phenomena (Ehrlich 1997). Yet much of the difficulty in grappling with the edge literature stems from the lack of a framework for understanding the patterns reported (Murcia 1995, Cadenasso et al. 2003) or comparing responses at the different edges present in a landscape (Ries & Sisk 2004). Determining how edge response patterns manifest at broader scales is also difficult, limiting most studies' utility for management and conservation (Sisk & Haddad 2002, Sisk et al. 2002, Battin & Sisk 2003). To clarify these issues, we present four major sections for this review:

1. A mechanistic model of edge responses. We synthesize ideas from the literature into a conceptual model of the fundamental mechanisms underlying

TABLE 1 A summary from a subset of studies measuring responses at forest edges showing the number of times positive, negative, neutral, or mixed results were observed[a]

Taxon	Number of studies[b]	Response variable	Pos	Neg	Neutral	Mixed[c]
Birds	10	Richness/diversity	2	0	3	5
	32	Abundance by species[d]	86	49	344	28
Plants	13	Richness/diversity	7	1	2	3
	16	Abundance by species[d]	85	30	167	9
Mammals	1	Richness/diversity	0	1	0	0
	20	Abundance by species[d]	12	6	25	9
Invertebrates	8	Richness/diversity	1	0	4	3
	10	Abundance by species[d]	6	7	70	11
Herps	1	Richness/diversity	0	1	0	0
	5	Abundance by species[d]	0	6	13	2
Abiotic	20	Several[e]	22	8	21	18

[a] Only studies that measured responses within forest edges adjacent to open habitat and met certain design criteria (see text) were included. See Appendix 1a for specific studies used.

[b] Only studies that met certain design criteria were included, see text for details.

[c] Studies reported more than one response (e.g., positive and neutral) for the same response variable when analyses were stratified by some factor.

[d] Summed tallies of all species reported in each study.

[e] For example, temperature, light levels, humidity, wind, soil properties, etc.

edge response patterns and describe the empirical evidence supporting each component of that model.

2. A predictive model of edge responses. We review a model that predicts how abundances change near edges and assess the ability of that model to account for variability described within the literature.
3. Interactions affecting edge responses. We review studies that identify ecological factors that interact with edge responses and determine how that variability can be understood within the framework of the above models.
4. Extrapolating edge responses to larger scales. We explore our ability to use edge response patterns to understand the distribution of organisms in heterogeneous landscapes.

To determine the strength of evidence for suggested patterns and mechanisms, we reviewed over 900 empirical papers on terrestrial edge responses located through database searches and from citations within papers. From those papers, we selected a subset for review on the basis of the following criteria: (*a*) distance to edge was an explanatory variable for analysis, (*b*) there was a minimum of three sampling replicates, (*c*) basic habitat descriptions were given for both sides of the edge, and (*d*) the adjacent patches among replicate study sites were similar in structure (i.e., all forest or all open). We imposed these criteria to ensure that studies were both comparable and relatively rigorous. Because studies on avian nest success have been thoroughly reviewed (see Paton 1994, Hartley & Hunter 1998, Lahti 2001, Chalfoun et al. 2002b), we did not include those empirical papers but instead present a synthesis of those reviews. These criteria resulted in 263 core papers used for our review of the empirical literature.

A MECHANISTIC MODEL OF EDGE RESPONSES

A Conceptual Framework

Researchers have invoked a broad range of mechanisms to explain changes in organism abundance near edges (Wiens et al. 1985, McCollin 1998, Fagan et al. 1999, Lidicker 1999, Cadenasso et al. 2003), yet a comprehensive framework has remained elusive (Murcia 1995, Ries & Sisk 2004). Here, we present a unified model of the mechanisms underlying edge effects on the abundance of organisms. From our review of the literature, we identified four fundamental mechanisms that change organismal abundance patterns across habitat edges: (*a*) ecological flows, (*b*) access to spatially separated resources, (*c*) resource mapping, and (*d*) species interactions. Ecological flows involve the movement of material, organisms, or energy between patches (Wiens et al. 1985, Cadenasso et al. 2003). Access to spatially separated resources may be enhanced near edges for organisms whose required resources are found in multiple habitat types (Leopold 1933, Dunning et al. 1992, McCollin 1998, Fagan et al. 1999). These first two mechanisms, flows and access, fundamentally alter habitat quality of edges relative to patch interiors. Habitat edges have maximum exposure to flows from adjacent patches and are the ideal location to gain access to spatially separated resources.

The final two mechanisms, resource mapping and species interactions, represent general ecological dynamics that, although not restricted to edges, are important components in an overall framework of how edges influence distributions. Resource mapping occurs when an organism's distribution reflects that of its resources. Species interactions describe any interspecific relationship that influences one or both species. In some cases (e.g., predator-prey interactions), an interaction constitutes resource use from one organism's point of view, causing overlap between the categories of resource mapping and species interactions. To avoid confusion, we define predator dynamics as species interactions from the perspective of the prey but resource mapping from that of the predator. Mutualisms and competition are considered under the category of species interactions. Although these four mechanisms capture most dynamics that influence edge responses, there may be some taxon-specific factors that do not fit easily into this, or any, general framework. For instance, the geometry of packing bird territories into patches may cause decreases in bird abundances near edges (passive displacement) that are not based on any change in habitat quality (King et al. 1997, Ortega & Capen 1999, Fletcher & Koford 2003).

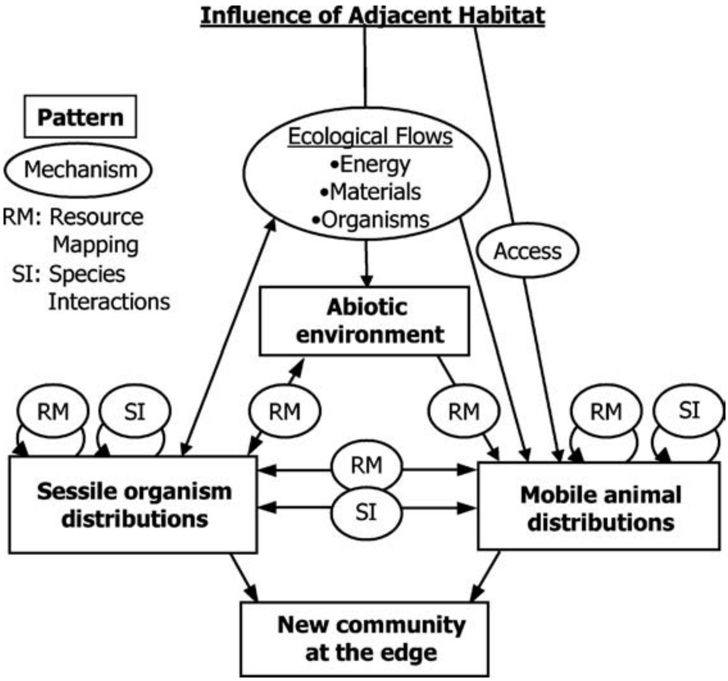


Figure 3 A mechanistic model describing the different pathways by which the distributions of organisms and, ultimately, community structure are altered near habitat edges. Patterns in the abiotic environment, mobile and sessile organism distributions, and community structure (*boxes*) are influenced by four fundamental mechanisms (*ovals*). Ecological flows of energy, material, and organisms across the edge influence the abiotic environment as well as organismal distributions. Mobile organisms whose resources are spatially separated can gain better access by being near edges. Organisms map onto changes in the distribution of their resources. Changes in species' distributions near edges can lead to novel species interactions that can further influence abundance and distributions. All these changes in species distribution lead to altered community structure near edges.

Figure 3 illustrates how these four mechanisms influence patterns in organismal distributions near habitat edges. We separate organisms into mobile and sessile groups because different pathways occur for each (specified below). Ecological flows influence mobile and sessile organisms directly by providing a source of materials and immigrants across edges. Indirect influences can also occur via organisms mapping onto changes in the abiotic environment near edges. However, only sessile organisms can feed back and directly influence ecological flows and the abiotic environment (note double-sided arrows in Figure 3 for those pathways). This feedback can occur either through changes in edge architecture that influence the permeability of the edge (Didham & Lawton 1999, Cadenasso et al. 2003) or by creating a gradient that affects the abiotic environment. Another factor that differentiates mobile from sessile organisms is that only mobile organisms are known to actively gain access to spatially separated resources in adjacent patches. Some sessile organisms may also demonstrate such responses if advantages at the edge can be realized via, for example, root or branch growth, but we are not aware of any examples demonstrating this effect. Instead, sessile organisms can gain access to resources associated with adjacent patches by being located near edges that receive flows from neighboring patches. Within the current edge literature, the categories of mobile and sessile organisms separate animals from plants and lichens, but that need not always be the case (for instance, many sessile aquatic organisms are animals). However, owing to this current dichotomy in the terrestrial literature, we formulate the bulk of our remaining discussion with respect to research on animals (mobile organisms) and plants or lichens (sessile organisms).

Finally, any change in a species' distribution may have cascading effects throughout the community (Figure 3). For example, changes in abiotic conditions near a habitat edge may lead to the establishment of new plant species, and previously absent animals may map onto these new resources, leading to novel interactions affecting multiple taxa and, ultimately, changing overall community structure (Figure 3). Below we review the evidence for each of the four mechanisms and, where possible, show how effects cascade throughout the community.

Empirical Evidence for Underlying Mechanisms

ECOLOGICAL FLOWS Ecological flows from adjacent habitat patches are a key mechanism underlying the distinction between edge and interior zones. The rate of ecological flows between patches is a function of edge permeability, the degree to which a given flow can penetrate the boundary between two patches. Edges can amplify, attenuate, or reflect ecological flows (Strayer et al. 2003). Edge permeability is strongly influenced by the architecture of the edge, largely on the basis of plant structure (Cadenasso et al. 2003). Changes in overstory cover can affect vertical penetration of light into a patch (Turton & Sexton 1996, Didham & Lawton 1999, Dignan & Bren 2003a), which may, in turn, affect temperature and humidity levels near the edge. The relative concentrations of energy, materials, and organisms on either side of the edge also affect flow rates. Materials that move passively may naturally diffuse to areas of lower concentration, but mobile organisms can move against natural gradients, making net flows more difficult to predict.

A number of studies have documented ecological flows from one patch into another. Microclimatic changes have been widely documented (e.g., Matlack 1993, Cadenasso et al. 1997, Burke & Nol 1998, Meyer et al. 2001) and are influenced by differential movement of light, heat, moisture, and wind from one patch to another (Weathers et al. 2001). The result of these differential flows is that environmental conditions near edges are often intermediate between conditions in both adjacent patch interiors. For instance, forest edges near open habitat are hotter, drier, and lighter than the forest interior (Chen et al. 1999). Conversely, open habitat near forest edges experiences increased shading, leading to lower temperatures and higher humidity (Cadenasso et al. 1997). Materials can be moved into adjacent habitat through diffusion, deposition, or the flow of animals (Cadenasso et al. 2003). Movement of animals across edges is widely documented in studies that quantify how edges mediate dispersal or influence movement direction (Sakai & Noon 1997, Haddad 1999, Ries & Debinski 2001, Schultz & Crone 2001, Matthysen 2002, Schtickzelle & Baguette 2003). The flow of plant propagules (seeds and pollen) across habitat edges has been demonstrated, but has received less study (Cadenasso & Pickett 2001, Cubiña & Aide 2001). In some cases, edges can act as relatively impermeable barriers that cause the accumulation of organisms or materials at the edge (e.g., Desrochers & Fortin 2000).

ACCESS Access is the other key mechanism that separates the quality of edge habitat from interior zones. When resources are spatially separated between two adjacent patches, edges provide maximum access to both resources (Dunning et al. 1992, McCollin 1998, Fagan et al. 1999). In his explanation of why edges should harbor higher densities of animals, Leopold (1933) used the example of bobwhite quail (*Colinus virginianus*), which use four different habitat types: forest, brushland, grassland, and agricultural fields. He suggested that quail should occur at higher densities in landscapes in which these four habitats are highly interspersed. In another early example, aspen experienced the heaviest outbreaks of a leaf-mining insect (*Lithocolletis salicifoliella*) near stands of coniferous trees, which are used as the insects' overwintering sites (Martin 1956). In perhaps the best-known example, brown-headed cowbirds (*Molothrus ater*), which parasitize the nests of forest-dwelling songbirds but forage in open pastures, often increase in abundance near forest edges (Lowther 1993). Access to different habitat types may be especially important to animals whose juvenile and adult forms have different habitat requirements (Martin 1956, Ponsero & Joly 1998). However, one must distinguish between cases in which resources in adjacent patches are different (complementary) from cases in which adjacent patches contain the same (supplementary) resources (Dunning et al. 1992), because in the latter case no edge response is expected.

RESOURCE MAPPING Resource mapping influences species distributions through more pathways than any other mechanism in our model (Figure 3). Any edge-related change in the distribution of an organism's resources may result in a concordant change in that organism's distribution. Although resource mapping is the most frequently studied mechanism, most studies are correlational and fail to establish that the variables being measured influence the abundance and distribution of the focal organism.

Both plants and animals map onto abiotic gradients, with microclimate (e.g., solar radiation, temperature, humidity, soil moisture) the most extensively documented. Several studies suggest that increased light levels near the forest edge cause changes in the plant community (Wales 1972, Honnay et al. 2002, Watkins et al. 2003), whereas studies on plant responses to nutrient gradients are rarer. Researchers have documented relationships between animal distributions and microclimate gradients (Burke & Nol 1998, Haskell 2000, Brotons et al. 2001, Fernandez-Juricic 2001, Schlaepfer & Gavin 2001). Lichens mapping onto tree distributions and liverworts mapping onto downed log distributions (Moen & Jonsson 2003) provide rare examples of sessile organisms mapping onto the distribution of other sessile organisms.

The most frequently studied mechanism for edge effects is resource mapping by animals onto plants, most commonly the relationship between bird distributions and vegetation structure, although most studies have not found evidence to support this mechanism (e.g., Ortega & Capen 1999, Fernandez-Juricic 2001, Beier et al. 2002, Fletcher & Koford 2003). Most of these studies, however, do not independently establish which vegetation characteristics are most directly related to bird distributions before they test for a correlation with distance to the edge. This approach limits the usefulness of these studies because animals are not expected to map onto gradients that do not influence the quality of their habitat. Kristan et al. (2003) provide a rare example of a study that independently tested the importance of different vegetation characteristics on bird and mammal distributions. They examined whether changes in those vegetation features near habitat edges could account for observed edge effects. They found that the abundance of two bird species and one mammal tracked changes in vegetation with respect to the edge, while another three species showed edge responses that were not related to vegetation (Kristan et al. 2003).

Animals mapping onto the distributions of other animals is also well studied. Spotted owls (*Strix occidentalis*) illustrate a clear example of a species whose edge response patterns are directly related to those of their prey. Spotted owls show increased abundances near edges when wood rats (*Neotoma* sp.) serve as their main prey (Zabel et al. 1995, Ward et al. 1998). Wood rats are more abundant at edges because they flow into forests from neighboring clearcuts, their primary habitat (Sakai & Noon 1997). In contrast, owls show no edge effect when their main prey base is flying squirrels (*Glaucomys sabrinus*), a species that shows no edge effect (Zabel et al. 1995). These and other examples demonstrate that organisms map onto gradients in their resources, but that researchers must identify the variables that most influence habitat quality before attempting to relate those variables to edge effects.

SPECIES INTERACTIONS Interactions in which one organism benefits at the expense of another (predation, parasitism, herbivory) are the most extensively studied class of species interactions within the edge literature, with the greatest attention paid to predation on bird nests. Edges are associated with increased nest predation and parasitism rates for birds, although most studies have found no edge effect on nest success, and a few have even found a decrease (see Paton 1994, Lahti 2001, Chalfoun et al. 2002b for reviews). These patterns may be influenced by the fact that most studies were conducted in only a few biogeographic regions (Tewksbury et al. 1998, Sisk & Battin 2002). Parasitism is also higher at edges for some amphibians (Schlaepfer & Gavin 2001) and mammals (Wolf & Batzli 2001). There is less evidence for consistent effects of predation and parasitism on invertebrates. Bird predation rates on the mantid species *Stagmomantis limbata* increased near edges, whereas parasitism rates were unaffected (Ries & Fagan 2003). Conversely, viral infections decreased near edges for the tent caterpillar *Malacosoma disstria* (Roland & Kaupp 1995), but Peltonen & Heliövaara (1999) found no edge effect in predation for bark beetles. Actively avoiding edges to escape predation pressure has been demonstrated most convincingly for mammals (Bowers & Dooley 1993, Jacob & Brown 2000, Wahungu et al. 2001, but see Morris 1997), with some evidence for amphibians (Schlaepfer & Gavin 2001). Birds show little evidence of avoiding predation pressure at edges, and some species may be unable to assess risk accurately (Gates & Gysel 1978, Schlaepfer et al. 2002, Battin 2004).

Predation on plants (herbivory and seed predation) is also well documented, with many studies finding higher predation levels at the edge (e.g., Restrepo & Vargas 1999, Roach et al. 2001, Donoso et al. 2003, Tallmon et al. 2003). For example, higher abundances of white-footed mice (*Peromyscus leucopus*) at forest-clearcut edges lead to higher seed predation rates for *Trillium ovatum*, an understory herb, decreasing recruitment and thus reducing population size near edges (Jules & Rathcke 1999, Tallmon et al. 2003). Other studies have documented the opposite pattern, showing that some herbivores avoid edges, leading to reduced seed predation rates (Ostfeld et al. 1997, Manson et al. 2001, Nickel et al. 2003).

Competitive interactions and mutualisms can also influence the distribution of organisms near edges, but empirical studies are relatively rare. Morgan (1998) found no evidence for a competitive interaction between native and exotic plants species. In contrast, Argentine ants (*Linepithema humile*) appear to outcompete the local, native ant species at some edges (Suarez et al. 1998). The noisy miner bird (*Manorina melanoecephala*) inhabits open areas and adjacent forest edges and drives many forest bird species away from the edge (Piper & Catterall 2003). In theory, edges may even reverse competitive interactions (an inferior competitor becomes the superior competitor) on the basis of the edge's permeability and of the difference in quality between adjacent patches (Cantrell et al. 1998), but there is no empirical evidence for this. Most examples of edge-related mutualisms involve animal-mediated pollination and seed dispersal. For instance, trillium recruitment is decreased near forest-clearcut edges because of lower pollination rates, which may be the result of lower pollinator abundance at edges (Jules & Rathcke 1999). The ecology of animal seed-dispersers also influences plant colonization rates and dispersal distances on the basis of the animal's movement rates (Brunet & von Oheimb 1998, Ingle 2003).

Summary

Our model presents four mechanisms (ecological flows, access, resource mapping, and species interactions) that capture most dynamics driving edge responses

(Figure 3). Whereas most studies investigate only one type of mechanistic pathway, our model clearly illustrates how edge effects may arise through multiple pathways. These different mechanisms may interact in complex ways to influence an individual species' distribution and, ultimately, community structure at an edge (Figure 3). A single edge effect may create a cascade of edge effects in a wide range of organisms (Wiens et al. 1985). For instance, alterations in light levels near an edge may increase the abundance of a plant that an herbivorous insect subsequently maps onto. This may cause a decrease in that insect's competitors and/or an increase in local predator densities. This example illustrates the potential pitfalls of using correlational studies to ascertain the actual mechanism driving observed abundance patterns. When two factors change concordantly with respect to the edge, one is often interpreted as being the mechanism for the other, when this may not be the case.

Without manipulating potential pathways, it is difficult to conclusively identify the mechanism most directly responsible for an observed edge response. However, the distribution of resources, as well as species interactions, are identified as the major drivers underlying edge responses (Figure 3). Therefore, one way to avoid spurious conclusions that may result from correlational studies is to know which resources and interactions are most important in driving the abundance patterns of each study organism. Studies of edge effects in which the variables that drive organism abundance are assessed independently from, as well as in association with, edges are much more powerful than strictly correlational studies (e.g., Ross et al. 1997, Kristan et al. 2003), but they are rare. Another way to avoid spurious conclusions is to have a priori predictions for the expected response of each organism at each edge type. We next review a predictive model based largely on the concepts and mechanisms illustrated in Figure 3 and show how it can make sense of patterns and variability reported in the edge literature.

A PREDICTIVE MODEL OF EDGE RESPONSES

Although the mechanistic model presented earlier (Figure 3) offers some clues to the conditions that lead to positive, negative, and neutral responses for a particular species at a particular edge type, it is not specifically predictive. Until recently (Brand 2004, Ries & Sisk 2004), no models had been presented that allow a researcher to predict changes in abundance near edges. Brand (2004) presents models that are specific to birds at forest edges, which we review later. Below, we focus on a more general model that predicts changes in abundance near edges for any species in any landscape (Ries & Sisk 2004). This predictive model is a simplification of the mechanisms illustrated in Figure 3 and is based primarily on resource distribution (Figure 4).

Predictions from this model (Figure 4) are based on relative habitat quality of adjacent patches and the distribution of resources within and between each patch (Ries & Sisk 2004). Habitat quality is defined by the relative availability of

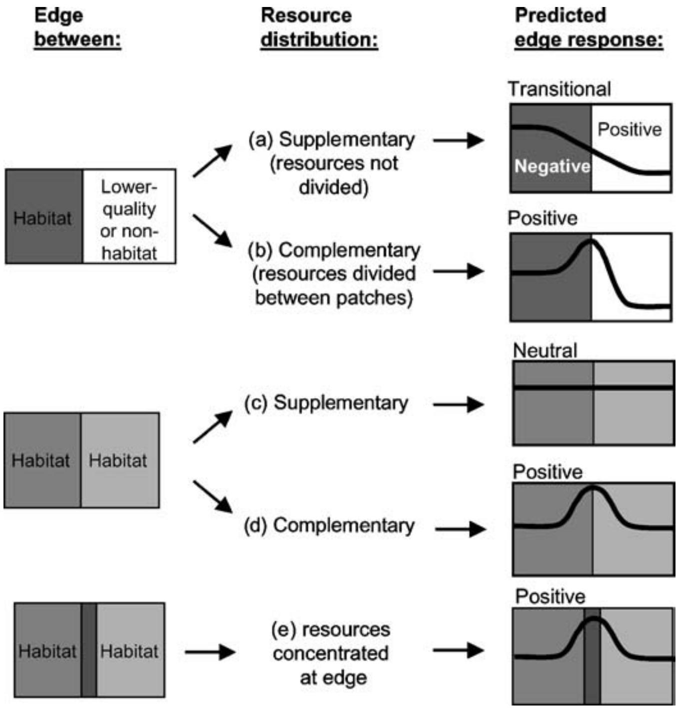


Figure 4 A predictive model of edge effects. This model is largely based on the mechanisms described in Figure 3. Edges are defined as the boundaries between patches, and patches are classified as habitat when they contain at least one resource, as nonhabitat when they contain no resources, and as lower-quality habitat when they contain fewer resources than the adjacent patch. When habitat borders nonhabitat or lower-quality habitat, where any available resources are (*a*) supplementary (the same) to those in the higher-quality patch, a transitional response is predicted. If there are resources in the lower-quality patch that are (*b*) complementary (different), then a positive edge response is predicted. When both patches contain resources, edge response predictions are based on whether the resources are (*c*) supplementary, which leads to a predicted neutral response, or (*d*) complementary in each patch, which leads to a positive prediction. When resources are (*e*) concentrated along the edge, a positive response is predicted. Reprinted with permission from Ries & Sisk (2004).

resources between the two patches. Patches are considered of lower quality when they contain fewer resources compared with the adjacent patch and nonhabitat when they contain no resources. Where organisms occur near nonhabitat or lower-quality patches, with supplementary resources (those that offer nothing different), organisms are predicted to decrease in abundance within higher-quality habitat near edges, although they may still spill over into the adjacent patch (Figure 4*a*).

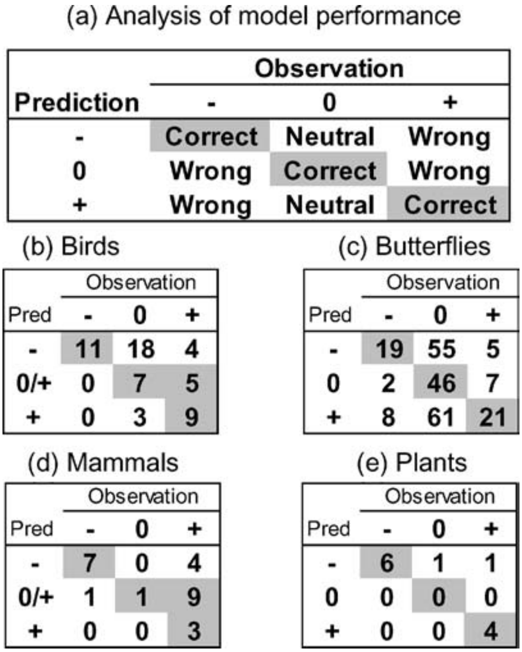
This spillover is due to flows of materials between patches (Figure 3) that tend to make edges more similar to adjacent patches and cause a gradual transition in habitat quality onto which organisms may map (Lidicker 1999). In contrast, if the lower-quality habitat contains resources that are complementary (different), then a positive response is predicted on both sides of the edge (Figure 4*b*) because access to all resources is increased near edges (Figure 3). When two adjacent patches contain relatively equal amounts of resources, no response is predicted when resources are supplementary (Figure 4*c*) because being near the edge confers no additional access to resources. Again, complementary resource distribution leads to a predicted increase near edges (Figure 4*d*) owing to increased access (Figure 3). Finally, if resources are concentrated along the edge, organisms may map onto the increase of their resources near edges (Figure 3) and are therefore predicted to increase (Figure 4*e*). One important implication of this model is that all species are predicted to show positive, neutral, and negative edge responses, depending on the edge type encountered. This may explain much of the inter- and intraspecific variability reported in the edge literature.

A Test of the Model on Several Taxa

To evaluate the general applicability of this edge response model, we compared predictions with observed responses for four taxa: birds, butterflies, mammals, and plants. Outcomes are divided into cases in which the model is correct and in which it is incorrect; however, we further divided incorrect outcomes into two distinct cases. We classified cases in which the model failed to predict a significant positive or negative edge response as a "wrong" prediction and cases in which the model predicted a positive or negative edge response, but no response was found as a "neutral" outcome (Figure 5*a*). This distinction allows separate evaluation of the factors that may have led to unpredicted neutral responses versus unpredicted positive and negative responses, outcomes that may have different underlying causes. In addition, neutral outcomes, although still incorrect, may have causes (e.g., lack of statistical power) that do not necessarily conflict with the underlying framework of the model.

Two tests of this edge response model have already been carried out. On the basis of a review of the bird literature (Ries & Sisk 2004), the model correctly predicted the direction of 83% of edge responses observed for more than 50 avian species at edges between forests and open habitat (Figure 5*b*). An intensive field study testing the predictions of the model was carried out for 15 butterfly species at 12 edge types (Ries 2003). The model performed well in all but one habitat type (which exhibited a high degree of internal heterogeneity). In the other four habitats investigated, when positive or negative predictions were made, observed edge responses were in the predicted direction 75% of the time (Figure 5*c*).

To determine how well the model performs for other taxa, we conducted a test for plants and mammals using our database of 263 papers (reptiles and amphibians



(a) Analysis of model performance

Prediction	Observation		
	-	0	+
-	Correct	Neutral	Wrong
0	Wrong	Correct	Wrong
+	Wrong	Neutral	Correct

(b) Birds

Pred	Observation		
	-	0	+
-	11	18	4
0/+	0	7	5
+	0	3	9

(c) Butterflies

Pred	Observation		
	-	0	+
-	19	55	5
0	2	46	7
+	8	61	21

(d) Mammals

Pred	Observation		
	-	0	+
-	7	0	4
0/+	1	1	9
+	0	0	3

(e) Plants

Pred	Observation		
	-	0	+
-	6	1	1
0	0	0	0
+	0	0	4

Figure 5 Analysis of the performance of the edge effect model (Figure 4). (*a*) Outcomes are separated into cases in which the model was correct and incorrect. Incorrect outcomes are further separated into two separate cases in which an unpredicted neutral response was observed and cases in which wrong positive or negative responses were observed. Results are presented for tests of the model on four taxa. (*b*) Bird results are from Ries & Sisk (2004). (*c*) Butterfly results are from Ries (2003). (*d*) Mammal and (*e*) plant results are from a review of the literature, and details for these tallies are given in Appendix 1b. (The Appendix is included as Supplemental Material. Follow the Supplemental Material link from the Annual Reviews home page at http://www.annualreviews.org.) Note that for birds and mammals, we lacked information to differentiate between positive and neutral predictions in some cases, so outcomes were identified as correct if either observation was recorded. Outcomes for which model predictions were correct are shaded in gray.

were not included because too few studies were available). This test allowed a determination of how generally applicable this model is across a wide variety of taxa and edge types. For both plants and mammals, we predicted a negative edge response when abundances were measured in the superior habitat and a positive response in lower-quality or nonhabitat (Figure 4*a*). Information on resource distribution (complementary versus supplementary) was rarely included, so for mammals, when a species was associated with both habitat types, either a neutral or positive (but not negative) response was predicted (see Figure 4*c*,*d*). This distinction was not necessary for plants because sessile organisms cannot generally gain access to resources in two separate patches. Observed edge responses were in the direction predicted by the model in 83% of cases for mammals (Figure 5*d*) and 91% for plants (Figure 5*e*). Papers used to test the model for mammals and plants are detailed in Appendix 1b (see Supplemental Material).

It is clear from these four tests (Figure 5*b*–*e*) that when edge responses are observed, they are largely predictable, even for different species at different edge types. Negative edge responses are due to individuals avoiding edges of low-quality habitat, and positive responses result when organisms gain access to resources either in adjacent patches or near edges. Some variability clearly remains unexplained; yet by using this model to isolate unpredicted responses, researchers can more easily focus on the remaining variability and attempt to account for it. Except for birds at forest edges (see below), there are no alternative predictive models with which to compare the performance of this model.

Accounting for Remaining Variation

For mammals, most unexplained variation comes from observing positive responses when negative ones were predicted (Figure 5*d*). This anomaly is potentially due to a lack of information on resource distribution, because a positive response would be predicted if complementary resources were known to occur in the less-preferred patch (Figure 4*b*) or if resources were concentrated along the edge (Figure 4*e*). Although resource distribution (either complementary, supplementary, or concentrated along the edge) is critical to the generation of more precise model predictions, this information is never as widely available as basic information on habitat associations. We therefore suggest that the relative distribution of critical resources on both sides of the edge should become standard information reported in edge studies.

For birds (Figure 5*b*) and butterflies (Figure 5*c*), most unexplained variation came from observing unpredicted neutral responses rather than unpredicted positive or negative "wrong" responses. One potential cause of these unpredicted neutral responses is that some species may be particularly insensitive to edges (Wiens et al. 1985, Lidicker 1999). Many species are often labeled as edge species, but this is likely due to a historical focus on a single edge type (forest edges). This labeling is especially true for birds, which are routinely classified as edge or interior species, as if such behaviors were consistent across all habitats and edge types. Although these classifications are under increasing challenge (Baker et al. 2002, Imbeau et al. 2003), they are still commonly used. Because the edge response model predicts that all species will show neutral responses at some edge types (Figure 4*c*), to gauge edge sensitivity accurately researchers must separate predicted neutral responses from unpredicted neutral responses. Only species that consistently fail to show edge responses where they are predicted should be considered edge insensitive. Currently, rigorous classification of any species as edge sensitive or insensitive is difficult. However, it would be useful to determine if some species are intrinsically less sensitive to habitat edges and, if so, if any life-history or ecological characteristics are associated with that insensitivity. Several characteristics, such as body size, mobility, and vulnerability to predation, have been suggested to influence overall sensitivity (Wiens et al. 1985, Lidicker 1999), although little evidence exists to substantiate these ideas.

Brand (2004) studied the ecological and life-history characteristics associated with edge responses in forest birds. In addition to habitat utilization characteristics (that closely mirror the predictions illustrated in Figure 4*a*,*c*), species are more likely to exhibit negative responses to forest-open edges if they require mesic conditions, have smaller body sizes, are less ecologically plastic, and have longer incubation and nestling periods (Brand 2004). Likewise, species are more likely to exhibit positive responses to the same forest edges if they nest in shrubs, have open cup nests, and are more ecologically plastic (Brand 2004). In the only other study of traits associated with edge sensitivity, Ries (2003) found that butterflies are more sensitive to edges if they are more vulnerable to predation and lighter in color (making them potentially more sensitive to microclimatic variation).

Another cause of unpredicted neutral responses is that most edge studies have low replication and therefore little power to detect any but the strongest responses (Murcia 1995). This problem is exacerbated by any ecological factor that interacts to weaken edge responses, a topic we explore in the following section. Finally, the predictive edge response model illustrated in Figure 4 is a necessary simplification of the complex pathways and different mechanisms presented in Figure 3. When unpredicted responses occur, it is useful to return to that underlying mechanistic framework and determine if critical resources were not considered, other species interactions were occurring, or complex pathways were not captured by the simplifying assumptions of this predictive model.

INTERACTIONS AFFECTING EDGE RESPONSES

Several studies have explored how a suite of ecological factors influence observed edge responses, and these studies allow insight into some of the unexplained variation described above. We review the four factors that have received the most attention: edge orientation, temporal effects, habitat fragmentation, and edge contrast. To explore these factors rigorously, we reviewed studies that measured edge responses for the same species at the same (or comparable) edge types while varying one of the above four factors. We then determined the percentage of times each factor influenced edge responses to cause the following four outcomes: (*a*) no interaction with edge responses; (*b*) expression, defined as a unidirectional edge response observed in some situations but not others; (*c*) strength, defined as changes in the magnitude of the effect or the distance it penetrates into the patch; or (*d*) direction, defined as an edge response switching direction from positive to negative or vice versa (see Figure 6).

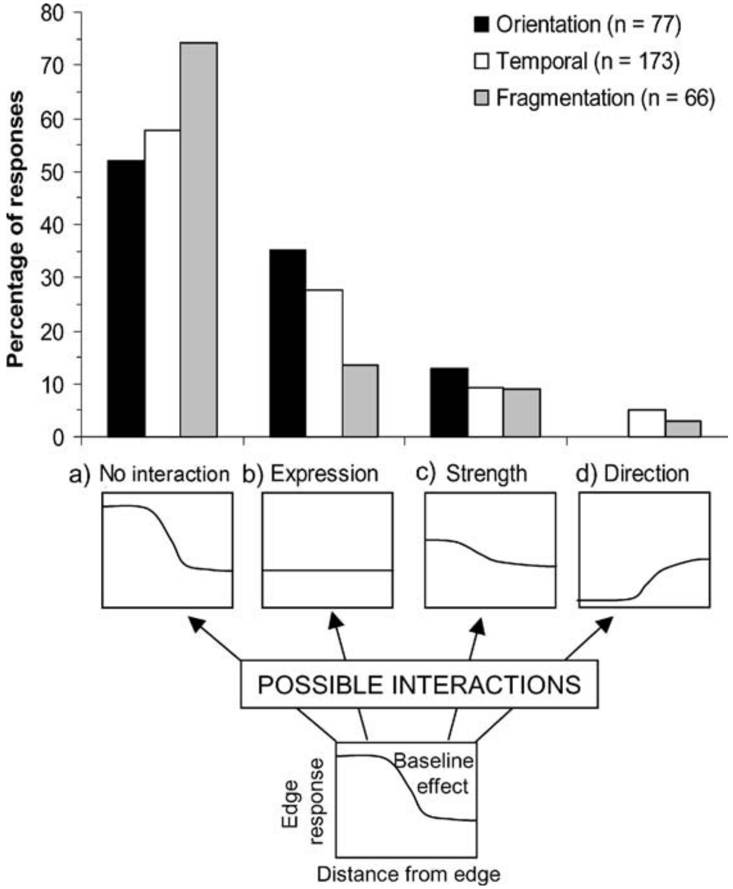


Figure 6 The influence of ecological factors that may interact to influence observed edge responses. Edge responses were compared within the same study for interactions on the basis of different orientations within the landscape, different temporal effects (daily, monthly, seasonally, or annually), and different levels of fragmentation. Outcomes of these comparisons fell into four classes. The ecological influences of orientation, time, or fragmentation either had (*a*) no interaction with observed edge responses, (*b*) caused an observed edge response not to be expressed, (*c*) changed the strength of an observed edge response, or (*d*) caused the observed edge response to change direction. The figure shows the percentage of times each outcome was observed. Details for each study are given in Appendix 1c.

Edge Orientation

The mechanistic model in Figure 3 indicates that the flow of energy is one of the fundamental drivers of edge responses. Because solar radiation is a major factor influencing the movement of energy, edges in different positions relative to the sun are likely to experience different rates, but not directions, of energetic flows (Matlack 1993, Dignan & Bren 2003b). Several studies have demonstrated that edge orientation can impact the strength or expression, but never the direction, of edge responses (Figure 6). Because edge orientation is rarely controlled for (Murcia 1995), it may be one cause of the unpredicted neutral responses reported earlier for the test of the edge response model, but not of the unpredicted positive and negative "wrong" responses (Figure 5).

If differential permeability to abiotic flows is the primary mechanism causing edge responses to weaken based on edge orientation, then we might expect two patterns. The first expected pattern is that orientation effects will be different in different latitudes. Specifically, in the northern temperate zones, south-oriented forest edges bordering open habitat should exhibit stronger edge effects (because of increased exposure to sunlight) than north-oriented edges. The converse should be true in the southern hemisphere (Kapos 1989, Young & Mitchell 1994), and little difference should be found in the tropics. These predictions may vary for other edge types, but only data on forest edges have been reported. There is strong support for the hypothesis that south-facing forest edges exhibit stronger edge responses in the northern temperate zone. When there were significant interactions in the northern hemisphere, edge responses were stronger or were expressed only at south-facing edges 42% of the time, compared with 3% at north-facing edges ($n = 67$). In the remaining cases, there was no interaction (Appendix 1c). Studies in the tropics and southern temperate zones were too rare to allow us to determine if patterns in those regions matched expectations.

The second expected pattern is that orientation will have a stronger influence on microclimatic patterns than on plant patterns and that the importance of orientation might continue to decrease through successively higher trophic levels. Orientation had a measurable effect on abiotic responses 63% of the time ($n = 19$), compared with only 42% of the time for plants ($n = 50$) (Appendix 1c), suggesting that damping may be occurring. Currently, there are too few studies on orientation effects on animals to determine if this damping effect occurs at higher trophic levels.

Temporal Effects

Temporal effects on edge responses have been investigated at a variety of scales, including time of day (Meyer et al. 2001), season (Young & Mitchell 1994), and year (Chalfoun et al. 2002a). Although these effects, particularly year effects, are often considered nuisance parameters, understanding their cause could help explain much of the observed variability in edge responses (Figure 6). Time most likely affects edge responses because of temporal patterns in resource distribution or use (Manson & Stiles 1998) that could vary either seasonally (Noss 1991, Young & Mitchell 1994) or throughout the day (Meyer et al. 2001). Predictable seasonal or daily change in resource use or distribution can be incorporated into the predictions of the edge response model (Figure 4) by stratifying predictions by season or time of day. Depending on how resource use or distribution changes temporally, it is even possible that the direction of an edge response could reverse, although these types of changes are rare (Figure 6*d*). Information on daily or seasonal changes in resource use or distribution are usually not reported, making this prediction difficult to test explicitly from the current literature. Year effects may also be driven by changes in resource distribution but are more difficult to predict than daily or seasonal effects because they likely originate from stochastic events, potentially driven by broad climatic patterns. Other temporal effects may originate from lag times in species responses, especially in sessile organisms with long generation times (e.g., Rose & Fairweather 1997) or from more gradual changes as the quality of the edge or adjacent patch changes through time.

Habitat Fragmentation

Fragmentation effects, which include patch size, isolation, and landscape composition, had the least effect on measured edge responses (Figure 6), although this pattern is strongly influenced by the results of one study (Moen & Jonsson 2003). When researchers did detect an interaction, the responses measured in one type of landscape were most commonly not expressed in another (Figure 6*b*). For example, brown-headed cowbirds are more likely to express edge responses in highly fragmented landscapes (Donovan et al. 1997), whereas black-tailed deer (*Odocoileus hemionus columbianus*) showed the opposite effect, with edge responses more likely when landscapes were less fragmented (Kremsater & Bunnell 1992). Many potential mechanisms are responsible for fragmentation influences on edge effects, and those mechanisms may be situation specific, making predictions difficult. Therefore, placing fragmentation interactions into a predictive framework may prove to be more difficult than for other factors discussed in this review.

Edge Contrast

Edge contrast may influence edge effects, and researchers generally assume that responses will be weaker near “soft” (low-contrast) edges than near “hard” (high-contrast) ones (Stamps et al. 1987, Duelli et al. 1990). Two main factors underlie differences in edge contrast: (*a*) differences in mean vegetation height between adjacent patches forming the edge, and (*b*) different vegetation densities within the same edge type. For both factors, differences in edge responses are likely due to differences in the permeability of the edge, resulting in different rates of ecological flows (Figure 3). Therefore, when differences in edge responses are due to edge contrast, the strength of the response is more likely to be affected than its direction. Few studies allow rigorous comparisons of edge contrast (so this factor is not included in Figure 6); however, results are similar to those presented earlier in that when a significant interaction is found, strength or expression is affected, but rarely direction.

The influence of edge contrast based on relative vegetation height is rarely rigorously explored because most studies do not control for differences in the relative qualities of the adjacent patches. This shortcoming is critical, because differences in adjacent habitat qualities are predicted to influence the strength of edge responses (Ries & Sisk 2004), and quality is often correlated with the degree of edge contrast, making these two factors particularly difficult to disentangle. Studies that have effectively controlled for habitat quality while varying edge contrast show mixed results. Fletcher & Koford (2003) found that grassland-dependent bobolinks (*Dolichonyx oryzivorus*) exhibited stronger edge avoidance near woodland edges (high contrast) than near rowcrop edges (low contrast), even though both constitute nonhabitat. Ries & Debinski (2001) found that the likelihood of a prairie endemic butterfly turning to avoid edges was stronger at high-contrast nonprairie edges than at low-contrast edges. In contrast, Ries (2003) found that edge contrast had no effect on the edge response of butterflies at several different kinds of riparian habitat edges.

The second type of edge contrast study, in which edge type is the same but vegetation structure in the focal habitat varies, is also rare but has received more rigorous treatment because the edges have been experimentally manipulated, a rarity in the edge literature. In the first example, the understory structure of a deciduous forest near an open edge was experimentally thinned. The change in vegetation density influenced whether edge responses were expressed for nutrient concentrations (Weathers et al. 2001) and rates of seedling herbivory by voles and deer (Cadenasso & Pickett 2000). The strength of edge responses varied for seed dispersal (Cadenasso & Pickett 2001). Likewise, Didham & Lawton (1999) compared relatively "open" and "closed" edges in experimentally created forest fragments in Brazil and found that edge responses were not expressed in closed-structure edges for canopy density, litter depth, or biomass, whereas edge responses changed direction for litter moisture.

Summary

The ecological factors examined rarely showed a significant interaction with edge responses (Figure 6*a*), but when they did, responses observed in one situation were either not expressed in another (Figure 6*b*) or the strength of the edge effect was modified (Figure 6*c*). In some cases, edge responses that were not observed may represent cases in which response strength was really affected but a lack of statistical power limited the ability to detect weaker patterns. The design of most edge studies, which often have low replication, few distance categories, and little penetration into patches, limits the detection of more subtle changes in edge response strength. In contrast, most edge studies are designed to capture differences in response direction, yet these cases are by far the least common outcome (Figure 6*d*). This fact suggests that changes in edge response direction for the same variable at the same edge type are rare occurrences. This pattern is encouraging and contrasts with the common conception that edge responses are intractably variable. It also suggests that, when edge responses are documented for specific species at specific edge types, managers can use this information as a generally reliable characteristic, with unforeseen shifts in the direction of edge responses unlikely to limit conservation strategies. Finally, interactions are often based on factors that are consistent with the models presented (Figures 3 and 4) and can therefore be either incorporated directly into predictions generated from the edge response model (Figure 4) or understood within the framework of our mechanistic model (Figure 3). Together, these models provide a tractable approach for understanding variability in edge responses.

EXTRAPOLATING EDGE RESPONSES TO LARGER SCALES

The main rationale cited for carrying out most edge studies is to understand better how landscape structure, usually fragmentation, influences the distribution and abundance of organisms. Although much progress has been made in describing how edges influence distributions at local scales, progress has been more limited in extrapolating measured responses to larger scales. This limited progress is unfortunate because knowledge of edge responses can contribute meaningfully to management and conservation strategies, particularly in landscapes undergoing rapid change (Sisk & Haddad 2002, Sisk et al. 2002, Battin & Sisk 2003). Few studies have tested how information on edge responses can be used to improve the understanding of distributions at larger scales (but see Temple 1986, Sisk et al. 1997, Haddad & Baum 1999).

Studies that are designed specifically to determine the role of edges as mechanisms underlying fragmentation-related patterns often demonstrate a direct link (Rosenberg & Raphael 1986, Roland 1993, Burke & Nol 1998, Didham et al. 1998, Bolger et al. 2000, Davies et al. 2001, Fletcher & Koford 2002). Furthermore, a formal meta-analysis of patch-size effects shows that species that avoid edges show increased densities in larger patches, and edge-attracted species show the opposite effect, whereas species that do not respond to edges show weak or no patch-size effects (Bender et al. 1998). This result suggests that edge responses are one of the main factors driving area sensitivity. Despite the obvious connection, three factors have limited researchers' ability to extrapolate edge responses to larger landscapes: (*a*) a lack of models and the software tools to implement them, (*b*) an incomplete knowledge of how deeply into patches edge effects extend, and (*c*) a poor understanding of how responses are influenced by the presence of multiple edges. We end this section with a brief discussion of how "scaling up" edge responses may help inform our understanding of population and community dynamics.

Models and Software Tools

Two primary models are used for "scaling up" edge responses to real landscapes: the core area model (Temple 1986, Laurance & Yensen 1991) and the effective area model (Sisk & Margules 1993, Sisk et al. 1997). Core area models use an estimated distance of edge influence to determine the amount of habitat in a patch that is not affected by edges (the core area). This model constitutes a significant advance in that it allows researchers to consider the portion of a landscape that is thought to be free of edge influences, and this model is often used when considering reserve designs (Temple & Cary 1988, Laurance 1991, Zipperer 1993, Ohman & Erikson 1998). Several software packages have the ability to measure the amount of core area in a landscape, facilitating the use of this approach. However, core area models have limited utility for species exhibiting variable responses to edges or in severely fragmented landscapes where most core habitat has already disappeared. The effective area model extends the core area approach by describing density (or other parameters) as a function of distance from edge, allowing researchers to generate quantitative predictions of distributions throughout an entire landscape. Furthermore, it allows researchers to specify different edge responses for each species at each unique edge type (Sisk et al. 1997, Sisk & Haddad 2002), thereby reflecting the complexity that exists in real landscapes (see Figure 1*b*). However, this model's use is currently limited by a lack of data for parameterization. Furthermore, software, although available, is at an early stage of development (Sisk et al. 2002).

Neither of the above models can incorporate variable edge responses based on landscape-level interactions, including edge orientation, patch size, or fragmentation effects (but see Zheng & Chen 2000). In the previous section, we demonstrated that these factors can interact to modify edge responses but that only strength or expression are generally affected, rarely the direction of the response (Figure 6). Edge responses are thus likely to manifest at larger scales in a predictable direction (Kolbe & Janzen 2002), but resulting magnitudes may be dampened depending on the extent to which orientation and landscape structure interact either to weaken edge responses or limit their expression.

Depth of Edge Influence

For both core area and effective area models, researchers must know the distance that edge effects extend into habitat patches. This value, often referred to as the depth of edge influence (DEI), is critical for determining the scale at which edge responses operate in larger landscapes (Laurance 2000). Although DEI values are reported for many edge responses, only recently have statistical techniques been suggested to allow for a rigorous determination of DEI (Fraver 1994, Cadenasso et al. 1997, Laurance et al. 1998, Mancke & Gavin 2000, Brand & George 2001, Harper & MacDonald 2001, Toms & Lesperance 2003). In many studies, DEI is determined by "visual inspection," and these numbers are likely influenced by study design (i.e., the length of survey transects and the number of distance categories). Without controlling for the statistical rigor of each study, abiotic and plant responses are generally reported to extend up to 50 m into patches, invertebrate responses up to 100 m, and bird responses 50–200 m (Appendix 1d). Examples of deeper DEIs exist for all classes, and Laurance (2000) suggested that some edge effects might occur over the scale of kilometers, yet most studies are not designed to capture effects at this scale. As empirical studies employ more rigorous designs

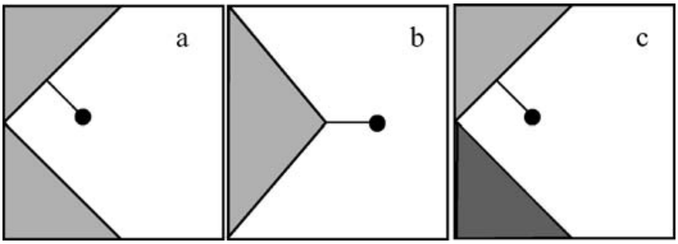


Figure 7 Complex and multiple edge effects. In most published studies, the influence of the edge is described for a point on the basis of the distance from that point to the nearest edge (shown by the dot and line), which is the same for all three panels in this figure (*a*, *b*, *c*). However, the type and strength of edge influence is likely to be different for each situation. Even at the same edge type (*a*, *b*), the geometry of the patch shape is likely to exhibit complex effects that cause edge influences to be either (*a*) greater or (*b*) lesser on points equidistant from the closest edge. A further complication that has received no empirical treatment is the convergence of multiple edge types at one point (*c*).

and statistical techniques, estimates of DEI can be more easily compared and used in landscape-level extrapolations.

Multiple Edge Effects

Another critical issue when extrapolating edge responses to landscapes is that most empirical research on edge effects has ignored the cumulative effect of being near more than one edge. Most studies (and models) use the linear distance to the closest edge as the main explanatory variable (Figure 7), and researchers generally avoid placing plots near corners or other converging edge types to limit their potential influence. However, complex patch geometry and the convergence of multiple edge types are dominant features of all real landscapes (see Figure 1*b*). If edge responses are different near multiple edges, then that factor should be incorporated into any model that extrapolates edge responses to complex landscapes. Multiple edge effects arising from complex patch geometry (Figure 7*a*,*b*) are poorly understood, yet they almost certainly influence the strength of edge effects by influencing both the magnitude and the depth of edge influence (Chen et al. 1995). For example, bobolinks exhibit a greater reduction in their probability of occurrence in plots located near corners compared with straight edges (Fletcher 2003). A further complication of multiple edge effects can arise when different edge types converge (Figure 7*c*), potentially causing complex edge responses on the basis of the relative influence of each adjacent habitat type (Fernandez et al. 2002). We know of no empirical studies that measure how edge responses are affected by the convergence of multiple habitat types. Mathematical approaches to deal with these issues have been suggested (Malcolm 1994, Mancke & Gavin

2000, Zheng & Chen 2000, Fernandez et al. 2002, Fletcher 2003), but the lack of empirical treatment severely limits our ability to understand how edge responses manifest in real landscapes.

Population and Community Consequences

Edge responses can also “scale up” to influence long-term population dynamics and community structure. The parameters that ultimately determine distributions (birth, death, immigration and emigration rates) are rarely modeled with respect to edges, which makes determining a cumulative influence of edges on population dynamics difficult. Edge effects may not have strong implications on population-level parameters, such as population growth rates, if the effect is weak or the response variable is not a limiting factor in population regulation. For example, Flaspohler et al. (2001) examined whether edge effects could affect population growth rates of ovenbirds. Although nest predation increased near edges, clutch size was higher, thereby offsetting predation and causing estimates of population growth rates to be similar for edge and interior habitats (see also Harris & Reed 2002). Also, the degree to which edges are important depends on the strength of the response and the relative amount of edge in a landscape (With & King 2001, Fletcher 2003). For these reasons, knowledge of edge responses may, in some cases, have limited utility in understanding population dynamics.

Although we have focused on individual species’ responses to edges, our mechanistic model shows that changes in individual species’ distributions ultimately culminate in an altered community at the edge (Figure 3). However, a framework for predicting community-level responses to habitat edges currently does not exist. Many studies have measured community changes near edges, with increases in species diversity the most common result (Table 1), but the causes and implications of changes in diversity near edges remain unclear. Increased diversity near edges could arise from an additive effect of species using each habitat type, increases of species using novel edge habitat, or some other emergent property. If increased diversity near edges is indeed a common and widespread pattern, the implications have received little exploration.

Summary

Despite decades of research describing how a suite of organisms respond to habitat edges, the tools to extrapolate edge responses to the landscape scale effectively and the specific data required to do so remain limited. Most studies are not designed to allow even the most basic models to be rigorously parameterized. Depth of edge influence is rarely quantified in a rigorous way, and the influence of multiple, complex edge effects has, for the most part, been ignored. This is unfortunate because understanding and predicting edge responses are clearly keys to understanding the impacts of fragmentation and other landscape-level changes. A recent review of the fragmentation literature (Fahrig 2003) admonished researchers to approach the study of fragmentation in a way that allows the impacts of habitat loss to be clearly separated from those of habitat structure. Understanding how edges impact patch quality is clearly one approach to meeting that important goal. A greater understanding of how edge responses influence population and community dynamics is also needed. Much work remains to be done to develop the knowledge and tools to accomplish this. Until these questions are more rigorously addressed, our ability to use edge response data to inform conservation and management issues remains limited.

CONCLUSIONS

Our review of the edge literature shows that the mechanisms underlying edge responses have been well described over several decades of research. The two models we present provide tools to make sense of a highly descriptive and variable literature. Our mechanistic model (Figure 3) illustrates four fundamental mechanisms underlying edge responses: ecological flows, access to spatially separated resources, resource mapping, and species interactions. These mechanisms form the basis of a general, predictive model of edge responses (Figure 4) that can be used for any species in any landscape. Our review of an extensive literature shows that edge responses, when observed, are generally predictable and consistent when species and edge type are held constant. This pattern contrasts with the generally held view that edge responses are largely idiosyncratic and based on disparate ecological phenomena. These models capture most variation, and additional variation can be explored by allowing researchers to focus on unpredicted outcomes. We identify several factors, including intrinsic sensitivity to edges, edge orientation, edge contrast, fragmentation effects, temporal shifts in resource distribution or use, and study design, that may influence observed edge responses. Finally, although many of the patterns and much of the variability in the current edge literature can be accounted for with these models, the tools necessary to extrapolate those responses to larger landscapes or to use them to understand population dynamics and community patterns have received less development, limiting our ability to use this information to inform conservation and management decisions in real, dynamic landscapes. We hope that this synthesis stimulates future research by allowing studies to be carried out under a theoretical, predictive framework. Edge responses are a key component in furthering our understanding of landscape-level dynamics, and their study continues to hold great promise in contributing even more to our growing understanding of how the spatial patterning of landscapes influences the abundance and distribution of organisms.

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LITERATURE CITED

Allen CD, Breshears DD. 1998. Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. *Proc. Natl. Acad. Sci. USA* 95:14839–42

Arris LL, Eagleson PS. 1989. Evidence of a physiological basis for the boreal-deciduous forest ecotone in North America. *Vegetatio* 82:55–58

Baker J, French K, Whelan RJ. 2002. The edge effect and ecotonal species: bird communities across a natural edge in southeastern Australia. *Ecology* 83:3048–59

Battin J. 2004. When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conserv. Biol.* In press

Battin J, Sisk TD. 2003. Assessing landscape-level influences of forest restoration on animal populations. In *Ecological Restoration of Southwestern Ponderosa Pine Forests*, ed. P Frederici, pp. 175–90. Washington, DC: Island

Beier P, Van Drielen M, Kankam BO. 2002. Avifaunal collapse in West African forest fragments. *Conserv. Biol.* 16:1097–111

Bender DJ, Contreras TA, Fahrig L. 1998. Habitat loss and population decline: a meta-analysis of the patch size effect. *Ecology* 79: 517–33

Bolger DT, Suarez AV, Crooks KR, Morrison SA, Case TJ. 2000. Arthropods in urban habitat fragments in southern California: area, age, and edge effects. *Ecol. Appl.* 10:1230–48

Bowers MA, Dooley JL. 1993. Predation hazard and seed removal by small mammals—microhabitat versus patch scale effects. *Oecologia* 94:247–54

Bowman D, Fensham RJ. 1991. Response of a monsoon forest-savanna boundary to fire protection, Weipa, northern Australia. *Aust. J. Ecol.* 16:111–18

Brand LA. 2004. *Prediction and assessment of edge response and abundance for desert riparian birds in southeastern Arizona*. PhD thesis. Colo. State Univ., Fort Collins

Brand LA, George TL. 2001. Response of passerine birds to forest edge in coast redwood forest fragments. *Auk* 118:678–86

Brittingham MC, Temple SA. 1983. Have cowbirds caused forest songbirds to decline? *BioScience* 33:31–35

Brotons L, Desrochers A, Turcotte Y. 2001. Food hoarding behaviour of black-capped chickadees (*Poecile atricapillus*) in relation to forest edges. *Oikos* 95:511–19

Brunet J, von Oheimb G. 1998. Migration of vascular plants to secondary woodlands in southern Sweden. *J. Ecol.* 86:429–38

Burke DM, Nol E. 1998. Influence of food abundance, nest-site habitat, and forest fragmentation on breeding ovenbirds. *Auk* 115:96–104

Cadenasso ML, Pickett STA. 2000. Linking forest edge structure to edge function: mediation of herbivore damage. *J. Ecol.* 88:31–44

Cadenasso ML, Pickett STA. 2001. Effect of edge structure on the flux of species into forest interiors. *Conserv. Biol.* 15:91–97

Cadenasso ML, Pickett STA, Weathers KC, Jones CG. 2003. A framework for a theory of ecological boundaries. *BioScience* 53:750–58

Cadenasso ML, Traynor MM, Pickett STA. 1997. Functional location of forest edges: gradients of multiple physical factors. *Can. J. For. Res.* 27:774–82

Callaghan TV, Crawford RMM, Eronen M,

Hofgaard A, Payette S, et al. 2002. The dynamics of the tundra-taiga boundary: an overview and suggested coordinated and integrated approach to research. *Ambio* 12:3–5

Cantrell RS, Cosner C, Fagan WF. 1998. Competitive reversals inside ecological reserves: the role of external habitat degradation. *J. Math. Biol.* 37:491–533

Chalfoun AD, Ratnaswamy MJ, Thompson FR. 2002a. Songbird nest predators in forest-pasture edge and forest interior in a fragmented landscape. *Ecol. Appl.* 12:858–67

Chalfoun AD, Thompson FR, Ratnaswamy MJ. 2002b. Nest predators and fragmentation: a review and meta-analysis. *Conserv. Biol.* 16:306–18

Chasko GG, Gates JE. 1982. Avian habitat suitability along a transmission-line corridor in an oak-hickory forest region. *Wildl. Monogr.* 82:1–41

Chen J, Franklin JF, Spies TA. 1995. Growing-season microclimatic gradients from clearcut edges into old-growth Douglas-fir forests. *Ecol. Appl.* 5:74–86

Chen J, Saunders SC, Crow TR, Naiman RJ, Brosofske KD, et al. 1999. Microclimate in forest ecosystem and landscape ecology. *BioScience* 49:288–97

Choesin D, Boerner REJ. 2002. Vegetation boundary detection: a comparison of two approaches applied to field data. *Plant Ecol.* 158:85–96

Clements FE. 1907. *Plant Physiology and Ecology*. New York: Holt

Cubiña A, Aide TM. 2001. The effect of distance from forest edge on seed rain and soil seed bank in a tropical pasture. *Biotropica* 33:260–67

Davies KF, Melbourne BA, Margules CR. 2001. Effects of within- and between-patch processes on community dynamics in a fragmentation experiment. *Ecology* 82:1830–46

Desrochers A, Fortin MJ. 2000. Understanding avian responses to forest boundaries: a case study with chickadee winter flocks. *Oikos* 91:376–84

Didham RK, Hammond PM, Lawton JH, Eggleton P, Stork NE. 1998. Beetle species responses to tropical forest fragmentation. *Ecol. Monogr.* 68:295–323

Didham RK, Lawton JH. 1999. Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. *Biotropica* 31:17–30

Dignan P, Bren L. 2003a. A study of the effect of logging on the understory light environment in riparian buffer strips in a southeast Australian forest. *For. Ecol. Manag.* 172:161–72

Dignan P, Bren L. 2003b. Modelling light penetration edge effects for stream buffer design in mountain ash forest in southeastern Australia. *For. Ecol. Manag.* 179:95–106

Donoso DS, Grez AA, Simonetti JA. 2003. Effects of forest fragmentation on the granivory of differently sized seeds. *Biol. Conserv.* 115: 63–70

Donovan TM, Jones PW, Annand EM, Thompson FR. 1997. Variation in local-scale edge effects: mechanisms and landscape context. *Ecology* 78:2064–75

Duelli P, Studer M, Marchand I, Jakob S. 1990. Population movements of arthropods between natural and cultivated areas. *Biol. Conserv.* 54:193–207

Dunning JB, Danielson BJ, Pulliam HR. 1992. Ecological processes that affect populations in complex landscapes. *Oikos* 65:169–75

Ehrlich PR. 1997. *A World of Wounds: Ecologists and the Human Dilemma*. Oldendorf/Luhe, Ger.: Ecology Inst.

Fagan WF, Cantrell RS, Cosner C. 1999. How habitat edges change species interactions. *Am. Nat.* 153:165–82

Fagan WF, Fortin MJ, Soykan C. 2003. Integrating edge detection and dynamic modeling in quantitative analyses of ecological boundaries. *BioScience* 53:730–38

Fahrig L. 2003. Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Syst.* 34:487–515

Fernández C, Acosta FJ, Abellá G, López F, Díaz M. 2002. Complex edge effect fields as additive processes in patches of ecological systems. *Ecol. Model.* 149:273–83

Fernández-Juricic E. 2001. Avian spatial segregation at edges and interiors of urban parks in

Madrid, Spain. *Biodivers. Conserv.* 10:1303–16

Flaspohler DJ, Temple SA, Rosenfield RN. 2001. Effects of forest edges on ovenbird demography in a managed forest landscape. *Conserv. Biol.* 15:173–83

Fletcher RJ. 2003. *Spatial and temporal scales of distribution and demography in breeding birds: implications of habitat fragmentation and restoration*. PhD thesis. Iowa State Univ., Ames

Fletcher RJ, Koford RR. 2002. Habitat and landscape associations of breeding birds in restored and native grasslands. *J. Wildl. Manag.* 66:1011–22

Fletcher RJ, Koford RR. 2003. Spatial responses of bobolinks (*Dolichonyx oryzivorus*) near different types of edges in northern Iowa. *Auk* 120:799–810

Fortin MJ. 1994. Edge detection algorithms for two-dimensional ecological data. *Ecology* 75:956–65

Fraver S. 1994. Vegetation responses along edge-to-interior gradients in the mixed hardwood forests of the Roanoke River basin, North Carolina. *Conserv. Biol.* 8:822–32

Gates JE, Gysel LW. 1978. Avian nest dispersion and fledging success in field-forest ecotones. *Ecology* 59:871–83

Haddad NM. 1999. Corridor use predicted from behaviors at habitat boundaries. *Am. Nat.* 153:215–27

Haddad NM, Baum KA. 1999. An experimental test of corridor effects on butterfly densities. *Ecol. Appl.* 9:623–33

Harper KA, MacDonald SE. 2001. Structure and composition of riparian boreal forest: new methods for analyzing edge influence. *Ecology* 82:649–59

Harris LD. 1988. Edge effects and conservation of biotic diversity. *Conserv. Biol.* 2:330–32

Harris RJ, Reed JM. 2002. Effects of forest-clearcut edges on a forest-breeding songbird. *Can. J. Zool.* 80:1026–37

Hartley MJ, Hunter ML. 1998. A meta-analysis of forest cover, edge effects, and artificial nest predation rates. *Conserv. Biol.* 12:465–69

Haskell DG. 2000. Effects of forest roads on macroinvertebrate soil fauna of the southern Appalachian mountains. *Conserv. Biol.* 14:57–63

Honnay O, Verheyen K, Hermy M. 2002. Permeability of ancient forest edges for weedy plant species invasion. *For. Ecol. Manag.* 161:109–22

Imbeau L, Drapeau P, Mönkkönen M. 2003. Are forest birds categorised as "edge species" strictly associated with edges? *Ecography* 26:514–20

Ingle NR. 2003. Seed dispersal by wind, birds, and bats between Philippine montane rainforest and successional vegetation. *Oecologia* 134:251–61

Jacob J, Brown JS. 2000. Microhabitat use, giving-up densities and temporal activity as short- and long-term anti-predator behaviors in common voles. *Oikos* 91:131–38

Johnston VR. 1947. Breeding birds of the forest edge in Illinois. *Condor* 49:45–53

Jules ES, Rathcke BJ. 1999. Mechanisms of reduced trillium recruitment along edges of old-growth forest fragments. *Conserv. Biol.* 13:784–93

Kapos V. 1989. Effects of isolation on water status of forest patches in the Brazilian Amazon. *J. Trop. Ecol.* 5:173–85

King DI, Griffin CR, DeGraaf RM. 1997. Effect of clearcut borders on distribution and abundance of forest birds in northern New Hampshire. *Wilson Bull.* 109:239–45

Kingston SR, Morris DW. 2000. Voles looking for an edge: habitat selection across forest ecotones. *Can. J. Zool.* 78:2174–83

Klasner FL, Fagre DB. 2002. A half century of change in alpine treeline patterns at Glacier National Park, Montana, USA. *Arct. Antarct. Alp. Res.* 34:49–56

Kolbe JJ, Janzen FJ. 2002. Spatial and temporal dynamics of turtle nest predation: edge effects. *Oikos* 99:538–44

Kremsater LL, Bunnell FL. 1992. Testing responses to forest edges: the example of black-tailed deer. *Can. J. Zool.* 70:2426–35

Kristan WB, Lynam AJ, Price MV, Rotenberry JT. 2003. Alternative causes of edge-abundance relationships in birds and small mammals of California coastal sage scrub. *Ecography* 26:29–44

Lahti DC. 2001. The "edge effect on nest predation" hypothesis after twenty years. *Biol. Conserv.* 99:365–74

Laurance WF. 1991. Edge effects in tropical forest fragments: application of a model for the design of nature reserves. *Biol. Conserv.* 57:205–19

Laurance WF. 2000. Do edge effects occur over large spatial scales? *Trends Ecol. Evol.* 15:134–35

Laurance WF, Ferreira LV, Rankin-De Merona JM, Laurance SG. 1998. Rain forest fragmentation and the dynamics of Amazonian tree communities. *Ecology* 79:2032–40

Laurance WF, Yensen E. 1991. Predicting the impacts of edge effects in fragmented habitats. *Biol. Conserv.* 55:77–92

Lay DW. 1938. How valuable are woodland clearings to birdlife? *Wilson Bull.* 50:254–56

Leopold A. 1933. *Game Management*. New York: Charles Scribner's Sons

Lidicker WZ. 1999. Responses of mammals to habitat edges: an overview. *Landsc. Ecol.* 14:333–43

Lowther PE. 1993. Brown-headed cowbird. In *The Birds of North America, No. 47*, ed. A Poole, F Gill. Philadelphia, PA: Birds N. Am.

Malcolm JR. 1994. Edge effects in central Amazonian forest fragments. *Ecology* 75:2438–45

Mancke RG, Gavin TA. 2000. Breeding bird density in woodlots: effects of depth and buildings at the edges. *Ecol. Appl.* 10:598–611

Manson RH, Ostfeld RS, Canham CD. 2001. Long-term effects of rodent herbivores on tree invasion dynamics along forest-field edges. *Ecology* 82:3320–29

Manson RH, Stiles EW. 1998. Links between microhabitat preferences and seed predation by small mammals in old fields. *Oikos* 82:37–50

Martin JL. 1956. The bionomics of the aspen blotch miner, *Lithocolletis salicifolia* Cham. (Lepidoptera: Gracillariidae). *Can. Ent.* 88:155–70

Matlack GR. 1993. Microenvironment variation within and among forest edge sites in the eastern United States. *Biol. Conserv.* 66:185–94

Matthysen E. 2002. Boundary effects on dispersal between habitat patches by forest birds (*Parus major, P. caeruleus*). *Landsc. Ecol.* 17:509–15

McCollin D. 1998. Forest edges and habitat selection in birds: a functional approach. *Ecography* 21:247–60

Meyer CL, Sisk TD, Covington WW. 2001. Microclimatic changes induced by ecological restoration of ponderosa pine forests in northern Arizona. *Rest. Ecol.* 9:443–52

Mills LS. 1995. Edge effects and isolation: red-backed voles on forest remnants. *Conserv. Biol.* 9:395–402

Moen J, Jonsson BG. 2003. Edge effects on liverworts and lichens in forest patches in a mosaic of boreal forest and wetland. *Conserv. Biol.* 17:380–88

Morgan JW. 1998. Patterns of invasion of an urban remnant of a species-rich grassland in southeastern Australia by non-native plant species. *J. Veg. Sci.* 9:181–90

Morris DW. 1997. Optimally foraging deer mice in prairie mosaics: a test of habitat theory and absence of landscape effects. *Oikos* 80:31–42

Murcia C. 1995. Edge effects in fragmented forests: implications for conservation. *Trends Ecol. Evol.* 10:58–62

Nickel AM, Danielson BJ, Moloney KA. 2003. Wooded habitat edges as refugia from microtine herbivory in tallgrass prairies. *Oikos* 100:525–33

Noss RF. 1991. Effects of edge and internal patchiness on avian habitat use in an old-growth Florida hammock. *Nat. Areas J.* 11:34–47

Ohman K, Eriksson LO. 1998. The core area concept in forming contiguous areas for long-term forest planning. *Can. J. For. Res.* 28:1032–39

Ortega YK, Capen DE. 1999. Effects of forest roads on habitat quality for ovenbirds in a forested landscape. *Auk* 116:937–46

Ostfeld RS, Manson RH, Canham CD. 1997. Effects of rodents on survival of tree seeds and seedlings invading old fields. *Ecology* 78:1531–42

Paton PWC. 1994. The effect of edge on avian nest success: How strong is the evidence? *Conserv. Biol.* 8:17–26

Peltonen M, Heliövaara K. 1999. Attack density and breeding success of bark beetles (Coleoptera, Scolytidae) at different distances from forest-clearcut edge. *Agric. For. Ent.* 1:237–42

Piper SD, Catterall CP. 2003. A particular case and a general pattern: hyperaggressive behavior by one species may mediate avifaunal decreases in fragmented Australian forests. *Oikos* 101:602–14

Ponsero A, Joly P. 1998. Clutch size, egg survival and migration distance in the agile frog (*Rana dalmatina*) in a floodplain. *Arch. Hydrobiol.* 142:343–52

Restrepo C, Vargas A. 1999. Seeds and seedlings of two neotropical montane understory shrubs respond differently to anthropogenic edges and treefall gaps. *Oecologia* 119:419–26

Ries L. 2003. *Placing edge responses into a predictive framework*. PhD thesis. North. Ariz. Univ., Flagstaff. 152 pp.

Ries L, Debinski DM. 2001. Butterfly responses to habitat edges in the highly fragmented prairies of central Iowa. *J. Anim. Ecol.* 70:840–52

Ries L, Fagan WF. 2003. Habitat edges as a potential ecological trap for an insect predator. *Ecol. Ent.* 28:567–72

Ries L, Sisk TD. 2004. A predictive model of edge effects. *Ecology.* In press

Roach WJ, Huntly N, Inouye R. 2001. Talus fragmentation mitigates the effects of pikas, *Ochotona princeps*, on high alpine meadows. *Oikos* 92:315–24

Roland J. 1993. Large-scale forest fragmentation increases the duration of tent caterpillar outbreak. *Oecologia* 93:25–30

Roland J, Kaupp WJ. 1995. Reduced transmission of forest tent caterpillar (Lepidoptera, Lasiocampidae) nuclear polyhedrosis virus at the forest edge. *Environ. Ent.* 24:1175–78

Rose S, Fairweather PG. 1997. Changes in floristic composition of urban bushland invaded by *Pittosporum undulatum* in northern Sydney, Australia. *Aust. J. Bot.* 45:123–49

Rosenberg KV, Raphael MG. 1986. Effects of forest fragmentation on vertebrates in douglas-fir forests. In *Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates*, ed. J Verner, ML Morrison, CJ Ralph, pp. 263–72. Madison: Univ. Wis. Press

Ross WG, Kulhavy DL, Conner RN. 1997. Stand conditions and tree characteristics affect quality of longleaf pine for red-cockaded woodpecker cavity trees. *For. Ecol. Manag.* 91:145–54

Sakai HF, Noon BR. 1997. Between-habitat movement of dusky-footed woodrats and vulnerability to predation. *J. Wildl. Manag.* 61:343–50

Saunders DA, Hobbs RJ, Margules CR. 1991. Biological consequences of ecosystem fragmentation: a review. *Conserv. Biol.* 5:18–32

Schilthuizen M. 2000. Ecotone: speciation-prone. *Trends Ecol. Evol.* 15:130–31

Schlaepfer MA, Gavin TA. 2001. Edge effects on lizards and frogs in tropical forest fragments. *Conserv. Biol.* 15:1079–90

Schlaepfer MA, Runge MC, Sherman PW. 2002. Ecological and evolutionary traps. *Trends Ecol. Evol.* 17:474–80

Schtickzelle N, Baguette M. 2003. Behavioural responses to habitat patch boundaries restrict dispersal and generate emigration-patch area relationships in fragmented landscapes. *J. Anim. Ecol.* 72:533–45

Schultz CB, Crone EE. 2001. Edge-mediated dispersal behavior in a prairie butterfly. *Ecology* 82:1879–92

Sisk TD, Battin J. 2002. Habitat edges and avian ecology: geographic patterns and insights for western landscapes. *Stud. Avian Biol.* 25:30–48

Sisk TD, Haddad NM. 2002. Incorporating the effects of habitat edges into landscape models: effective area models for cross-boundary management. In *Integrating Landscape Ecology into Natural Resource Management*, ed. J Liu, W Taylor, pp. 208–40. Cambridge, UK: Cambridge Univ. Press

Sisk TD, Haddad NM, Ehrlich PR. 1997. Bird assemblages in patchy woodlands: modeling the effects of edge and matrix habitats. *Ecol. Appl.* 7:1170–80

Sisk TD, Margules CR. 1993. Habitat edges and restoration: methods for quantifying edge effects and predicting the results of restoration efforts. In *Nature Conservation 3: Reconstruction of Fragmented Ecosystems*, ed. DA Saunders, RJ Hobbs, PR Ehrlich, pp. 57–69. Sydney, Aust.: Surrey, Beatty & Sons

Sisk TD, Noon BR, Hampton HM. 2002. Estimating the effective area of habitat patches in heterogeneous landscapes. In *Predicting Species Occurrences: Issues of Accuracy and Scale*, ed. JM Scott, PJ Heglund, ML Morrison, pp. 713–25. Washington, DC: Island

Smith TB, Wayne RK, Girman DJ, Bruford MW. 1997. A role for ecotones in generating rainforest biodiversity. *Science* 276:1855–57

Stamps JA, Buechner M, Krishnan VV. 1987. The effects of edge permeability and habitat geometry on emigration from patches of habitat. *Am. Nat.* 129:533–52

Strayer DL, Power ME, Fagan WF. 2003. A classification of ecological boundaries. *BioScience* 53:723–29

Suarez AV, Bolger DT, Case TJ. 1998. Effects of fragmentation and invasion on native ant communities in coastal southern California. *Ecology* 79:2041–56

Tallmon DA, Jules ES, Radke NJ, Mills LS. 2003. Of mice and men and trillium: cascading effects of forest fragmentation. *Ecol. Appl.* 13:1193–203

Temple SA. 1986. Predicting impacts of habitat fragmentation on forest birds: a comparison of two models. In *Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates*, ed. J Verner, ML Morrison, CJ Ralph, pp. 301–4. Madison: Univ. Wis. Press

Temple SA, Cary JR. 1988. Modeling dynamics of habitat-interior bird populations in fragmented landscapes. *Conserv. Biol.* 2:340–47

Tewksbury JJ, Hejl SJ, Martin TE. 1998. Breeding productivity does not decline with increasing fragmentation in a western landscape. *Ecology* 79:2890–903

Toms JD, Lesperance ML. 2003. Piecewise regression: a tool for identifying ecological thresholds. *Ecology* 84:2034–41

Turton SM, Sexton GJ. 1996. Environmental gradients across four rainforest-open forest boundaries in northeastern Queensland. *Aust. J. Ecol.* 21:245–54

Villard MA. 1998. On forest-interior species, edge avoidance, area sensitivity, and dogmas in avian conservation. *Auk* 115:801–5

Wahungu GM, Catterall CP, Olsen MF. 2001. Predator avoidance, feeding and habitat use in the red-necked pademelon, *Thylogale thetis*, at rainforest edges. *Aust. J. Zool.* 49:45–58

Wales BA. 1972. Vegetation analysis of north and south edges in a mature oak-hickory forest. *Ecol. Monogr.* 42:451–71

Ward JP, Gutiérrez RJ, Noon BR. 1998. Habitat selection by northern spotted owls: the consequences of prey selection and distribution. *Condor* 100:79–92

Watkins RZ, Chen J, Pickens J, Brosofske KD. 2003. Effects of forest roads on understory plants in a managed hardwood landscape. *Conserv. Biol.* 17:411–19

Weathers KC, Cadenasso ML, Pickett STA. 2001. Forest edges as nutrient and pollutant concentrators: potential synergisms between fragmentation, forest canopies, and the atmosphere. *Conserv. Biol.* 15:1506–14

Wiens JA, Crawford CS, Gosz JR. 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. *Oikos* 45:421–27

Wilcove DS. 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* 66:1211–14

With KA, King AW. 2001. Analysis of landscape sources and sinks: the effect of spatial pattern on avian demography. *Biol. Conserv.* 100:75–88

Wolf M, Batzli GO. 2001. Increased prevalence of bot flies (*Cuterebra fontinella*) on white-footed mice (*Peromyscus leucopus*) near forest edges. *Can. J. Zool.* 79:106–9

Yahner RH. 1988. Changes in wildlife communities near edges. *Conserv. Biol.* 2:333–39

Young A, Mitchell N. 1994. Microclimate and vegetation edge effects in a fragmented podocarp-broadleaf forest in New Zealand. *Biol. Conserv.* 67:63–72

Young ND. 1996. An analysis of the causes of genetic isolation in two Pacific Coast iris hybrid zones. *Can. J. Bot.* 74:2006–13

Zabel CJ, McKelvey K, Ward JP. 1995. Influence of primary prey on home-range size and habitat-use patterns of northern spotted owls (*Strix occidentalis caurina*). *Can. J. Zool.* 73:433–39

Zheng DL, Chen JQ. 2000. Edge effects in fragmented landscapes: a generic model for delineating area of edge influences (D-AEI). *Ecol. Model.* 132:175–90

Zipperer WC. 1993. Deforestation patterns and their effects on forest patches. *Landsc. Ecol.* 8:177–84

(a) A simplified view of edges between habitat and non-habitat in a "fragmented" landscape

(b) Edges are more complex when the same landscape is viewed in the context of a mosaic of different patches

Figure 1 Dark green patches show the distribution of old-growth long-leaf pine (*Pinus pilustrus*) on a section of Ft. Benning in Georgia, USA. These pine stands are habitat for the red-cockaded woodpecker (*Picoides borealis*), an endangered species restricted to the Southeast. In the top panel (*a*), habitat is illustrated in a classic "fragmentation" context, where all patches are portrayed as either habitat (*dark green*) or nonhabitat (*white*). In fact, the surrounding landscape forms a complex mosaic (*b*) that has multiple influences on each patch. Lighter greens represent younger pine age classes, yellow patches are open or brushy habitat, brown represents hardwood stands, orange is mixed hardwood-pine stands, and purple is areas developed for military use. The influence of these different types of patches, experienced largely as "edge effects," can be as varied as the types of patches found within the landscape. Forest stand maps are used with permission of Ft. Benning.