Conservation Biology

Essay

Edge-Effect Interactions in Fragmented and Patchy Landscapes

LAUREN M. PORENSKY* AND TRUMAN P. YOUNG

Department of Plant Sciences and Graduate Group in Ecology, University of California, Davis, CA 95616, U.S.A., email lporensky@cabnr.unr.edu

Abstract: *Ecological edges are increasingly recognized as drivers of landscape patterns and ecosystem processes. In fragmented and patchy landscapes (e.g., a fragmented forest or a savanna with scattered termite mounds), edges can become so numerous that their effects pervade the entire landscape. Results of recent studies in such landscapes show that edge effects can be altered by the presence or proximity of other nearby edges. We considered the theoretical significance of edge-effect interactions, illustrated various landscape configurations that support them and reviewed existing research on this topic. Results of studies from a variety of locations and ecosystem types show that edge-effect interactions can have significant consequences for ecosystems and conservation, including higher tree mortality rates in tropical rainforest fragments, reduced bird densities in grassland fragments, and bush encroachment and reduced wildlife densities in a tropical savanna. To clarify this underappreciated concept and synthesize existing work, we devised a conceptual framework for edge-effect interactions. We first worked to reduce terminological confusion by clarifying differences among terms such as* edge intersection *and* edge interaction. *For cases in which nearby edge effects interact, we proposed three possible forms of interaction: strengthening (presence of a second edge causes stronger edge effects), weakening (presence of a second edge causes weaker edge effects), and emergent (edge effects change completely in the presence of a second edge). By clarifying terms and concepts, this framework enables more precise descriptions of edge-effect interactions and facilitates comparisons of results among disparate study systems and response variables. A better understanding of edge-effect interactions will pave the way for more appropriate modeling, conservation, and management in complex landscapes.*

Keywords: boundary, corridor, habitat fragmentation, heterogeneous landscapes, landscape connectivity, landscape ecology, linkage, matrix

Interacciones del Efecto de Borde en Paisajes Fragmentados

Resumen: *Los bordes ecológicos cada vez más son reconocidos como conductores de patrones del paisaje y de procesos del ecosistema. En paisajes fragmentados (e.g., un bosque fragmentado o una sabana con montículos de termitas dispersos), los bordes pueden ser tan numerosos que sus efectos permean en todo el paisaje. Resultados de estudios recientes en tales paisajes muestran que los efectos de borde pueden ser alterados por la presencia o proximidad de otros bordes cercanos. Consideramos la significancia teórica de las interacciones de los efectos de borde, identificamos varias configuraciones paisajísticas que las soportan y revisamos la investigación existente sobre este tópico. Los resultados de estudios de una variedad de tipos de localidad y ecosistema muestran que las interacciones del efecto de borde pueden tener consecuencias significativas para los ecosistemas y la conservación, incluyendo tasas de mortalidad de árboles más altas en bosques tropicales, densidades reducidas de aves en fragmentos de pastizal, y la intrusión de arbustos y densidades bajas de vida silvestre en una sabana tropical. Para clarificar este concepto subestimado y*

**Current address: Department of Natural Resources and Environmental Science, University of Nevada, Reno 89557, NV, U.S.A., email lporensky@cabnr.unr.edu*
Paper submitted August 27, 2012; revised manuscript accepted November 1, 2012.

Conservation Biology, Volume 27, No. 3, 509–519

DOI: 10.1111/cobi.12042

sintetizar el trabajo existente, diseñamos un marco conceptual para las interacciones del efecto de borde. Primero trabajamos para reducir la confusión terminológica mediante la clarificación de diferencias entre términos como la intersección de borde *y la* interacción de borde*. En casos en que interactúan los efectos de borde cercanos, propusimos tres formas de interacción posibles: reforzamiento (la presencia de un segundo borde causa mayores efectos de borde), debilitamiento (la presencia de un segundo borde causa efectos de borde más débiles) y emergente (los efectos de borde cambian completamente en la presencia de un segundo borde). Con la clarificación de términos y conceptos, este marco de referencia permite descripciones más precisas de las interacciones del efecto de borde y facilita la comparación de resultados entre sistemas y variables de respuesta dispares. Un mejor entendimiento de las interacciones del efecto de borde allanará el camino para el modelaje más adecuado, la conservación y manejo de paisajes complejos.*

Palabras Clave: borde, conectividad del paisaje, conexión, corredor, ecología del paisaje, fragmentación del hábitat, paisajes heterogéneos

Introduction

Ecological edges are boundaries or transition zones between two adjacent landscape patches or land cover types (Cadenasso et al. 2003). Such edges can modify a broad range of ecological parameters, including abiotic properties, species distributions, and species interactions (e.g., Young et al. 1995; Fagan et al. 1999; Ries et al. 2004). These modifications, or edge effects, can have important implications for the structure, function, and management of complex landscapes (Harper et al. 2005; Laurance 2008).

Edge effects display considerable variability among study systems (Murcia 1995; Ries et al. 2004) and among sites within a given study system (Laurance et al. 2007). Some of this observed variability is linked to variability in landscape context (Ries et al. 2004; Laurance et al. 2007). For example, edge-effect patterns in the same study system can differ on the basis of size and shape of different landscape patches (Collinge & Palmer 2002; Smith et al. 2010). Edge effects can also differ on the basis of matrix type or quality (Sisk et al. 1997; Pauchard & Alaback 2004; Santos-Barrera & Urbina-Cardona 2011), degree of contrast between adjacent patches (Collinge & Palmer 2002; Campbell et al. 2011), structure of the edge itself (Cadenasso et al. 2003), and other contextual factors (Matlack 1994; Chen et al. 1995). Moreover, edge effects at the same location can differ dramatically across different response variables (Cadenasso et al. 1997).

Despite this rich body of work on edges and their context dependence, research on some facets of landscape context is still limited. In particular, relatively little is known about what happens when multiple edges are near one another in patchy landscapes. Recent studies show that edge effects can be altered by the presence or proximity of other, nearby edges (Fig. 1 & Table 1). This phenomenon—interaction among multiple nearby edge effects (hereafter edge interaction)—is beginning to be recognized as a potentially important driver of ecological dynamics in complex landscapes (Ries et al. 2004; Laurance et al. 2007).

Edge interactions are ecologically important because they can affect interpretation of and broad-scale applicability of findings from studies on single edges. Results from studies of single edges are often used to predict the effects of a variable number or density of edges at a broader or coarser scale (e.g., predicting the effects of forest fragmentation on the abundance of an endangered forest specialist). In many cases, focal landscapes span a gradient from highly intact to highly fragmented (e.g., Fletcher 2005). Although edges become much more numerous across this gradient, many researchers do not consider interactions among nearby edges. In particular, the modeled spatial extent of edge influence, often represented by a buffer width, tends to be held constant as landscapes become more fragmented (e.g., Forman & Godron 1981; Laurance & Yensen 1991). If edge effects do change as edges get closer together, the predictions of many such models—and their conservation and management implications—will be inaccurate.

Changes in land use often increase the probability and prevalence of edge interactions. For example, fragmentation tends to promote edge interactions by producing landscapes with smaller patches and more complex patch shapes (e.g., Fletcher 2005). Linear and point-source disturbances (e.g., roads, oil rigs, water holes) in large

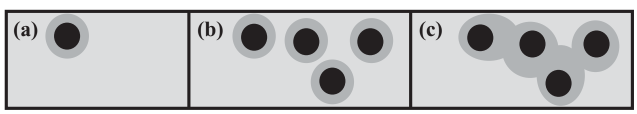

Figure 1. Effects of edge interaction in a hypothetical landscape: (a) landscape with a relatively degraded or low-quality (for a given species) matrix (light gray), a high-quality patch (black), and a medium-quality edge (dark gray); (b) landscape with four high-quality patches and noninteracting medium-quality edges; (c) landscape as in (b) except that edge interactions increase the amount and connectivity of medium-quality edge. Differences in edge-effect depth are illustrated, but shifts in edge-effect magnitude are also possible.

Table 1. Summary of empirical research on edge interactions.[a]

Study location	*Adjacent patch types*	*Edge treatment (more vs. less potential for edge interaction)*	*Response variable*	*Edge interaction*	*Reference*
New Jersey, U.S.A.	hedgerow, crops	linear planting vs. intersection with a second linear planting (Fig. 2c)	herbaceous plant species diversity	yes: strengthening	(Forman & Godron 1986)
Lowland farms in Britain	hedgerow, pasture or crops	linear planting vs. intersection with a second linear planting (Fig. 2c)	bird abundances	yes: strengthening	(Lack 1988)
Near Manaus, Brazil	tropical rainforest, pasture or regrowth	fragment corners vs. fragment edges (Fig. 2b)	overstory and understory vegetation thickness	yes: strengthening	(Malcolm 1994)
North Hampshire, U.K.	hedgerow, crops	field corner (created via hedgerow intersection) vs. field edge (Fig. 2b)	carabid beetle abundances	yes: strengthening	(Joyce et al. 1999)
Near Manaus, Brazil	tropical rainforest, pasture or regrowth	fragment corners vs. fragment edges (Fig. 2b)	liana abundance and diversity	no: nonsignificant result	(Laurance et al. 2001)
Near Manaus, Brazil	tropical rainforest, pasture or regrowth	fragment corners vs. fragment edges (Fig. 2b)	tree species richness and community similarity	yes: strengthening	(Benitez-Malvido & Martinez-Ramos 2003)
Near Manaus, Brazil	tropical rainforest, pasture or regrowth	fragment corners vs. fragment edges (Fig. 2b)	tree mortality, density, species richness, and community composition	yes: strengthening	(Laurance et al. 2006)
Iowa, U.S.A.	temperate grassland, crops	fragment corners vs. fragment edges (Fig. 2b)	breeding bird density	yes: strengthening	(Fletcher 2005)
Alberta & Quebec, Canada	temperate forest, clear-cut and lake	narrow vs. wide forest corridors (Fig. 2d)	density of logs, saplings, snags, and live trees; canopy cover	yes: strengthening and weakening	(Harper et al. 2007)
New South Wales, Australia	replanted forest, pasture or crops	linear planting vs. intersection with a second linear planting (Fig. 2c)	bird species richness, bird abundances	yes: strengthening	(Lindenmayer et al. 2007)
Laikipia, Kenya	tropical savanna, nutrient-rich treeless glades	closely spaced glades vs. more distant glades (Fig. 2e)	tree density and size structure, understory plant cover and diversity, *Acacia* ant community, wildlife density and diversity	yes: strengthening, weakening, and emergent	(Porensky 2011)

[a] *Findings and biological consequences of these studies are discussed more thoroughly in Supporting Information.*

patches (Laurance et al. 2009) are also likely to produce edge interactions.

Given their potential prevalence and ecological effects, edge interactions need greater attention. We synthesized what is known about edge interactions and devised a useful way to conceptualize and study them. Specifically, we examined landscape configurations that may enhance edge interactions, reviewed existing empirical research on edge interactions, and devised a conceptual framework for edge interactions.

Landscape Configurations that Support Edge Interactions

Edge interactions are possible in diverse situations. We considered landscape configurations that tend to put multiple edges in proximity to each other and therefore support edge interactions. We focused our examples on edges that separate more intact from more degraded patches because most studies of edge effects contrast patches that are more versus less disturbed by anthropogenic activities. For example, many commonly studied edge effects occur between roads and natural areas or between fields and forests (e.g., Harper et al. 2005). Fragmentation studies tend to focus on the proliferation of these types of edges. However, edge interactions can also occur in complex human-dominated landscapes (e.g., suburbia) and naturally patchy landscapes such as savannas with scattered termite mounds (Pringle et al. 2010), rooting zones where multiple roots pass through blocks of soil (Belnap et al. 2003), or streambeds with multiple patches of leaf litter (Wiens 2002).

We focused on landscapes with only two patch types, although many real situations are more complex (Li et al. 2007). Harper et al. (2007) detected edge interactions in a landscape with three focal patch types and two edge types. We know of no empirical studies in which interactions among three or more edge types were explored (see also Ries et al. 2004). In landscapes with two dominant patch types, four types of edge interactions (differentiated on the basis of patch configuration [Fig. 2]) are likely to occur: inward, outward, inward nucleating, and outward nucleating.

Inward edge interactions can occur when intact or restored patches—or portions of such patches—within a more-degraded matrix are small enough or narrow enough that the edge effects from their different sides interact. This situation can apply to small, isolated fragments (Fig. 2a), narrow fragments such as landscape linkages or hedgerows (Fig. 2a), corners of larger fragments where adjacent edges converge (Fig. 2b), or narrow portions of patches with convoluted edges (Fig. 2c).

Outward edge interactions can occur when anthropogenic features break up large intact patches and effectively produce smaller or narrower patches. This situation can apply to linear anthropogenic features such as roads, canals, and rights of way that cross larger blocks of land (Fig. 2d) or point-source disturbance features that are close enough for their edges to interact (Fig. 2e).

Above, we focused on situations where edge effects of degraded patches penetrated into more intact patches. However, relatively intact patches can also have edge effects that penetrate into more degraded patches. Inward-nucleating edge interactions can occur when degraded patches—or portions of such patches—within a more-intact matrix are small enough or narrow enough that the edge effects from their different sides interact (Fig. 2f & 2g).

Outward-nucleating edge interactions can occur when small intact patches (often remnant) dissect a degraded matrix and are close enough to one another that their edges can interact across the matrix (Fig. 2h). This includes remnant trees in clearcut areas and isolated trees that serve as perches for seed-dispersing birds and bats (see also Fig. 2c in Young [2000]).

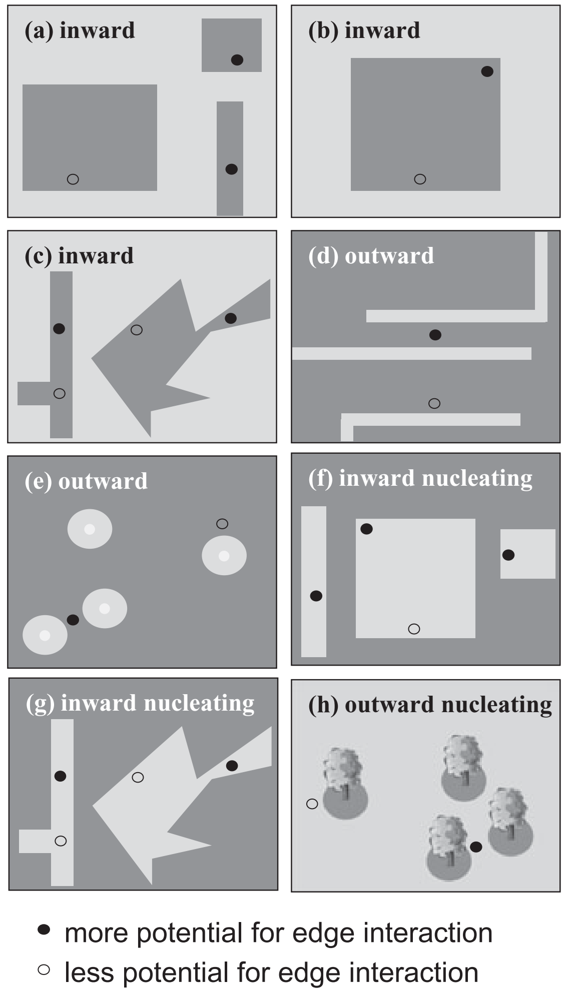

Figure 2. Aerial views of hypothetical landscapes with potential for edge interaction. Open black circles are near edges with less potential for edge interaction, closed black circles are near edges with more potential for edge interaction, dark gray areas are intact habitat, and light gray areas are degraded habitat for a species of interest. Inward interactions are likely in (a) small or narrow intact patches, (b) patch corners, or (c) narrow regions of complex patches. Outward interactions are likely when large intact patches contain features such as (d) roads or (e) water holes. Inward-nucleating interactions are likely when degraded patches (or portions of such patches) are (f) small, narrow, or (g) convoluted. Outward-nucleating interactions are likely when (h) small intact patches have edge effects that radiate outward across a degraded matrix.

We believe researchers and managers can use these categories to identify different types of edge interaction within a given landscape. When doing so, it is important to recognize that study questions and study organisms will inform both the delineation of patch boundaries (and therefore patch configuration) and the definition of patches as intact or degraded. Patches that are intact for one species, community, or researcher may be considered degraded for a different species, community, or researcher. Moreover, every edge effect that penetrates into one patch is radiating outward with respect to the adjacent one (i.e., both patches have edge effects). Because of this, complex landscapes often have the potential to simultaneously support multiple types of edge interaction. For example, consider roads of different widths that cross a large forested patch. Nearby roads may cause outward edge interactions that affect the intervening forest (Fig. 2d). However, the two edges of a single road are also likely to be interacting with each other, especially in the case of narrower roads (inward-nucleating interactions, Fig. 2f & 2g). The likelihood of multiple types of edge interactions increases with landscape complexity. In simpler landscapes (e.g., a remnant forest patch surrounded by a large pasture), it is more likely that when two edges intersect, their proximity makes the two landscape types asymmetrical, in that only one landscape type is located between two patches or blocks of the other type. Some edge effects are penetrating toward the area of intersection, whereas others are penetrating away from it. Edge interactions should be most dramatic in the area of intersection.

Finally, the presence or significance of edge interactions may itself depend on aspects of landscape context. For example, Harper et al. (2007) found that the specific identities of nearby patches affected the strength of edge interactions. Similarly, edge interactions may be sensitive to edge contrast, structure, and orientation, all of which are known to affect single-edge effects (Chen et al. 1995; Cadenasso et al. 2003; Reino et al. 2009).

Summary of Existing Research on Edge-Effect Interactions

Three terms are used commonly to describe edge effects: *shape*, *depth*, and *magnitude* (Supporting Information) (Cadenasso et al. 1997; Harper et al. 2005; Ewers & Didham 2006). Edge response shape is the functional form of the response curve across an edge (e.g., sigmoid or unimodal) (Ewers & Didham 2006). Edge-effect depth (or distance) has been defined in numerous ways, but broadly it represents the physical distance to which effects of one patch penetrate an adjacent patch (Chen et al. 1992; Harper et al. 2005; Harper & Macdonald 2011). Edge-effect magnitude is the amount of change in a given response variable across an edge (Harper et al. 2005) and can be quantified as the difference between the average values measured in adjacent patches or the difference between the maximum and minimum values measured across the edge region. Together, these three parameters provide a fairly thorough description of most edge effects (Supporting Information) (Ewers & Didham 2006).

We differentiated among approaches used to study edge interactions on the basis of their ability to measure and compare edge-effect depth, magnitude, and response shape. We advocate the use of approaches that can quantify these parameters because they enable clear, objective comparisons between different response variables, patch types, scales, studies, and landscape contexts (Ewers & Didham 2006). We also used edge-effect parameters as the building blocks for our conceptual framework.

Assumption of No Interaction

A common approach to multiple edge effects is one in which highly fragmented landscapes become "all edge" (e.g., Forman & Godron 1981; Howell et al. 2007). Edge effects are often conceptualized as step functions with a particular depth. When landscapes are sufficiently fragmented, the entire intervening area becomes uniformly affected by edges. In the "all edge" model it is generally assumed that nearby edges do not interact: depth, magnitude, and shape of edge effects remain constant as edge density increases. An all-edge model is appropriate only if the edge-effect response shape is indeed a step function and if edge interactions are negligible. However, in most cases the all-edge model is a simplification. Most edge effects decrease gradually as distance from the edge increases (Ewers & Didham 2006) and edge interactions may be common in complex landscapes (Table 1).

Empirical Evidence for Edge Interactions

Recent work has moved beyond the all-edge model. We know of 11 studies that present quantitative empirical data on edge interactions while controlling for potentially confounding factors (e.g., patch area). Ten of these studies provide support for the idea that edges interact (Table 1). Significant ecological consequences of edge interactions in existing work include higher tree mortality rates in tropical rainforest fragments, reduced bird densities in grassland fragments, and signs of bush encroachment (including reduced wildlife densities) in a tropical savanna (Supporting Information). Although the relative paucity of studies on this topic may reflect a bias against publishing negative results (Lortie et al. 2007) or an inability to overcome the statistical power issues associated with broad-scale research, we believe it is more likely that edge interactions have only recently begun to be studied. The latter explanation is supported by the fact that existing studies have detected edge interactions for a variety of biological entities in a variety of ecosystems and landscape types (Table 1).

To test for edge interactions directly, researchers have compared edge effects near a single edge with edge effects near (or between) multiple edges. The definition of a *single edge* is study- and system-specific and may be relative rather than absolute (i.e., farther from vs. closer to other edges). Moreover, like single-edge effects, edge interactions must be defined in relation to each individual response variable (Cadenasso et al. 1997). To avoid confounding edge interactions with changes caused by differences in patch size or core area (i.e., region of the patch unaffected by edges), researchers working in small fragments have generally compared edge effects at different locations within the same fragment (Fig. 2b & 2c). For example, locations near fragment corners are close to two edges, whereas locations far from corners are only close to one edge. In situations where water holes, roads, or other features fragment a large patch (Fig. 2d-f) authors have identified edge interactions by altering the distance between two fragmenting features. For example, in the absence of edge interaction, a patch containing two water holes separated by a large distance should have a similar amount of total and core area as a patch containing two water holes separated by a small distance.

After identifying appropriate edge treatments (single edge vs. multiple edges), researchers have used a variety of different strategies to quantitatively compare edge effects across treatments. The simplest approach has been to measure a response variable at a given distance from the edge in two different regions of the same patch: one region with more edge influence and one with less. With this approach one cannot differentiate among modifications of edge response shape, depth, or magnitude because data are only collected at one distance from the edge. For example, in three studies edge effects were compared between rainforest fragment corners (two converging edges) and fragment edges (Laurance et al. 2001; Benitez-Malvido & Martinez-Ramos 2003; Laurance et al. 2006). All these studies measured traits of plant communities at a given distance from the edge in plots close to versus far from corners. In four additional studies, researchers used a similar approach to study networks of linear vegetation strips (Forman & Godron 1986; Lack 1988; Joyce et al. 1999; Lindenmayer et al. 2007). In these studies response values were compared at a set distance from the edge in locations either far from or close to the intersection between one planting and a second planting (Table 1).

In the first example of a more complex approach, Malcolm (1994) developed a model that predicted vegetation thickness at a given location within a rainforest fragment by formally integrating edge effects produced at each point along the fragment's boundary. Malcolm found that field data more closely matched output from a model which included edge interactions than output from a model which did not. Fernandez et al. (2002) later expanded Malcolm's model to accommodate more complex edge response shapes and spatially variable edge effects. In both models the assumption is that edge interactions are arithmetically additive (Supporting Information), although the models could probably be adapted to include different interaction types. Arithmetically additive edge interactions produce simultaneous changes in the magnitude and depth of edge effects, but usually no change in response shape (Supporting Information). Although these integration-based models are powerful, they require data of relatively high spatial resolution and are therefore difficult to apply in many empirical situations.

More recently, Fletcher (2005) used a slightly simpler approach to study breeding Bobolink (*Dolichonyx oryzivorus*) densities in grassland fragments. For each bird observed in a fragment, the author calculated its distance to the nearest edge and, for plots near fragment corners, its distance to the next-nearest edge. This approach allowed Fletcher to plot edge response shapes (i.e., bird occurrence as a function of distance to the edge or edges) and test how both the magnitude and depth of edge effects differed between single- and multiple-edged plots.

Harper et al. (2007) also measured response variables at multiple distances from the edge, which allowed the authors to plot edge response shapes. The authors used a randomization test approach to compare edge effects observed between two nearby edges to edge effects predicted from single-edge data.

Porensky (2011) identified edge interactions with a nonlinear modeling method that was based on the continuous response function approach developed by Ewers and Didham (2006). Edge-effect parameters were extracted from fitted nonlinear models and compared statistically between single-edge and multiple-edge treatments. We believe the methods used by Fletcher (2005), Harper et al. (2007), and Porensky (2011) are preferable to other approaches because they allow quantification of edge-effect parameters with relatively moderate amounts of field data and do not assume additive edge interactions.

Results of 10 of the 11 existing studies show that edge interactions led to significantly stronger edge effects for some response variables (Table 1 & Supporting Information). However, results of two studies show that edge interactions also led to significantly weaker edge effects for some response variables, and results of one study show edge interactions can fundamentally alter edge response shapes (Table 1 & Supporting Information). These findings illustrate the difficulties associated with using data from single edges to predict the effects of multiple edges in patchy landscapes.

Additional Evidence and Tools

Results of several studies show that edge effects are sensitive to changes in patch size or shape (e.g., Mancke & Gavin 2000; Collinge & Palmer 2002; Nemethova &

Tirinda 2005; Ewers et al. 2007; Smith et al. 2010). Edge interactions could help explain these findings because edge interactions are more likely in smaller and more convoluted patches (Fig. 2a-c). However, altered edge effects in such studies could also have been driven by other mechanisms associated with changes in patch size or shape, such as Allee effects or disproportionate loss of core area. Unlike these studies, the examples described above used creative approaches to isolate edge interactions while holding other factors constant.

Finally, two studies used GIS-based simulations to investigate how edge interactions could alter the ecology of fragmented landscapes (Li et al. 2007; LaCroix et al. 2008). The spatially explicit models used in these studies could probably be expanded so that edge-effect parameters could vary continuously across a landscape in response to contextual factors (e.g., other nearby edges or edge orientation). This type of approach will prove especially useful once simulations are linked to empirical edge-interaction data. To our knowledge, only Lack (1988) and Fletcher (2005) used their edge-interaction results to inform broad-scale land-cover conversion scenarios.

A Conceptual Framework

At the current stage of research on edge interactions, a conceptual framework is needed to synthesize the diverse findings of existing studies and to make future findings easier to explain and compare. We propose that in fairly simple landscapes (such as those considered thus far in empirical studies) there are only a few general classes of edge interactions. Below, we describe these classes with a common and consistent vocabulary and illustrate how the different classes are connected (Fig. 3). Our ideas here have benefited from previous conceptual thinking on this and related topics (e.g., Fletcher 2005; Ewers & Didham 2006; Harper et al. 2007).

Historically, the use of confusing terminology has made it difficult to clearly describe edge interactions and compare findings among studies. For example, the word *additive* has been used in two different ways to describe edge interactions. In strict mathematical terms, additive interactions occur when two edges intersect and the value of a response variable is the arithmetical sum of the two values of single-edge effects at their respective distances (Supporting Information) (e.g., Malcolm 1994; Mancke & Gavin 2000). However, *additive* is often used more loosely to mean that in areas of edge overlap, the contribution of both edges to a particular response variable is greater than the contribution of only one edge (usually the nearest one). This latter usage, which encompasses subadditive, additive, multiplicative, and other interactions, appears to be more common (e.g., Laurance et al. 2007). These different uses of *additive* interfere with understanding what authors mean when they say that edges interact additively.

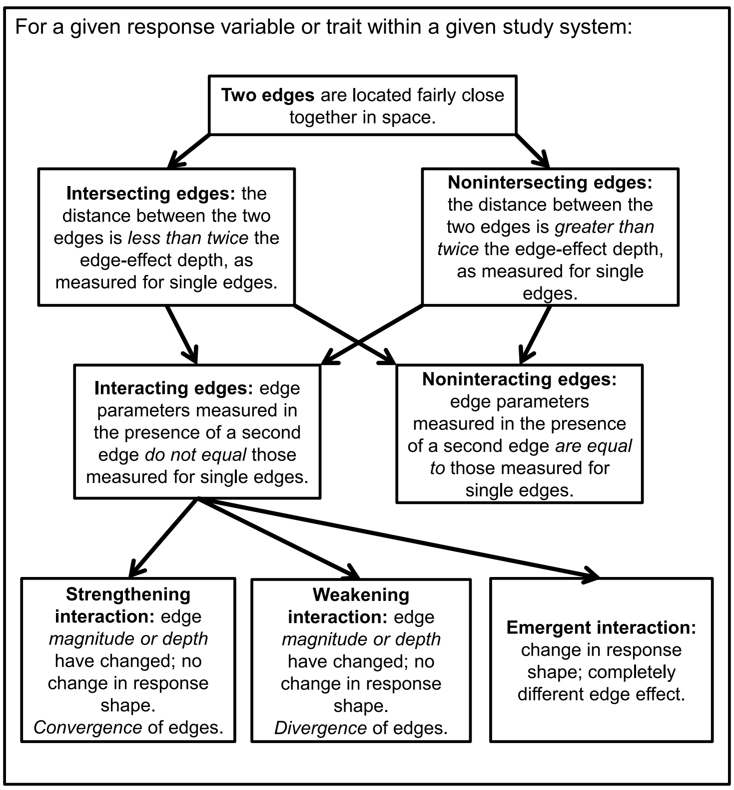

Figure 3. Conceptual framework illustrating classes of edge interactions and the ways they are connected.

The terms *positive* and *negative* can also be used in several ways when describing edge interactions. For example, consider the boundary between a forest and a pasture. Tree density is higher in the forest than the pasture (a sigmoid response). Now, consider what happens when the forest is reduced to a narrow corridor between two pastures. Edge interaction may lead to increased tree mortality at the forest edge (a result observed by Laurance et al. [2006]). This would typically be considered an additive interaction of the two field edges, despite the fact that tree density was reduced. This interaction could be considered *positive* because edge interaction led to stronger edge effects or *negative* because tree density declined.

A third terminological issue can be illustrated by assuming that before fragmentation, deer density was highest in the edge between the forest and the pasture (a unimodal response). When the forest is reduced to a narrow fragment, maximum deer density at the forest-pasture edge may decline (perhaps due to the loss of complementary resources [e.g., Ries et al. 2004]). However, density values may still remain higher in the forest than the pasture across the width of the fragment. Thus, the presence of a second edge caused a shift in edge response shape from unimodal to sigmoid. It is difficult to categorize this type of interaction using existing terminology (i.e., additive, positive, negative).

We devised a framework and vocabulary (Fig. 3) that can be used less ambiguously and regardless of edge response shapes or values. We based this framework on the edge-effect parameters described above (edge response shape, edge-effect magnitude, and edge-effect depth). Thanks to substantial methodological advances (reviewed by Harper et al. 2005; Ewers & Didham 2006), these edge-effect parameters can now be quantified for a wide variety of edges. Moreover, edge-effect parameters can be compared across studies and systems. Edge-effect parameters are specific to a response variable or trait of interest (Cadenasso et al. 1997), and this framework is therefore trait or response specific.

Edge Intersection versus Edge Interaction

Edge intersection is defined by physical distance: two edges are intersecting when the distance between them is smaller than twice the edge-effect depth as measured at single edges. *Edge interaction* occurs when the presence or proximity of a second edge alters the depth, magnitude, or shape of an edge effect. In other words, when edges interact, the physical distance to the closest edge is no longer an accurate predictor of the response value.

Edge intersection and edge interaction can occur independently. First, intersecting edges may not interact (Supporting Information). In many cases, results obtained from single edges will hold regardless of the presence or proximity of additional edges. In such cases, broad scale models based solely on single-edge data would be appropriate.

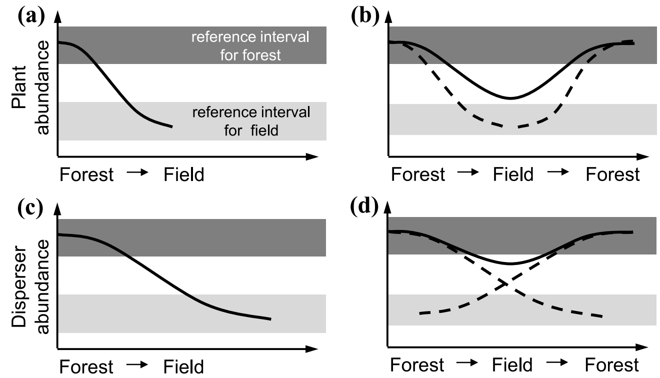

Figure 4. Edges that interact without intersecting. For a landscape in which the abundance of a given plant species (response variable) is higher in forests than fields, plant abundance may (a) have a relatively small edge-effect depth and (b) be significantly elevated between two nearby forest patches despite the fact that the distance between the two forest patches is greater than twice the edge-effect depth (as shown in [a]). Such a result could be driven by (c) an ecologically linked response variable with a larger edge-effect depth (e.g., abundance of a dispersal agent). For disperser abundance, the two nearby forest patches may have (d) edge effects that both intersect and interact. Elevated disperser abundance between nearby patches could lead to elevated plant abundance in this region. In (b) and (d), dashed lines are single-edge response patterns and solid lines are expressed patterns.

Second, edges may interact without intersecting. In at least one study, edge effects were altered by the presence of a second edge even when this second edge was far away relative to the depth of the single-edge effect (Porensky 2011). Edge interactions across large distances likely resulted from the activities of large animals that perceived the landscape at a broader scale. As this example suggests, edge effects that interact without intersecting are likely to be mechanistically linked to the edge effects of other response variables that have greater edge-effect depths and for which edges do intersect (Fig. 4). This potentially important situation does not fit within the traditional understanding of how edges interact (i.e., edges can interact only when they intersect). If edges interact without intersecting, models that assume arithmetically additive or multiplicative interactions will be inappropriate.

Strengthening and Weakening Interactions

Strengthening interactions occur when the presence of a second edge increases the effect size of a single edge by altering edge-effect magnitude, increasing edge-effect depth, or both (e.g., Malcolm 1994; Fletcher 2005). For a response with a monotonic (e.g., sigmoid) edge response shape, strengthening interactions lead to the merging or convergence of nearby patches. For a response with a unimodal shape, strengthening interactions cause the response peak to become wider or higher (or a trough to become deeper). Defined in this way, strengthening interactions encompass all types of additive interactions. We propose that *additive* be used only in the strict mathematical sense (Supporting Information) and then only as *arithmetically additive*. The term *strengthening* allows for either an increase or a decrease in the actual response value, thus avoiding any potential confusion associated with the terms *positive* and *negative*. Moreover, strengthening interactions can either increase or decrease edge-effect magnitude, depending on the edge response shape (Supporting Information). Finally, strengthening interactions can include cases in which the presence of a second edge leads to an increase in edge-effect depth even when it does not alter edge-effect magnitude.

Weakening interactions are the converse of strengthening interactions. Weakening interactions occur when the presence of a second edge decreases the effect size of a single edge by altering edge-effect magnitude, reducing edge-effect depth or both (e.g., Harper et al. 2007; Porensky 2011). For a response with a monotonic (e.g., sigmoid) shape, weakening interactions lead to the divergence of nearby patches. For a response with a unimodal shape, weakening interactions cause the response peak to become narrower or shorter. Weakening interactions are possible in a variety of situations, although the mechanisms driving them may not be as intuitive as those driving strengthening interactions. For example, Harper et al. (2007) found that clearcutting generated weaker edge effects (e.g., less blowdown) when the clearcut edge was close to a lakeshore edge. The authors hypothesized that the presence of a lakeshore could be associated with a higher percentage of wind-resistant trees in nearby forest areas. Due to the presence of these wind-resistant trees, a cut edge close to a lake may experience less blowdown than a cut edge far from a lake (Supporting Information). In a field dominated by edge effects that reduce diversity or hinder function, the possibility of weakening interactions may be heartening. Such interactions could help maintain high-quality habitat (for a given species or set of species) in small patches or narrow linkages.

Emergent Interactions

Emergent interactions occur when edge response shape is altered by the presence of a nearby edge in ways not describable in terms of strengthened or weakened single-edge effects. In other words, the fundamental nature of a single-edge effect is altered by interaction between edges. A change in shape may also involve changes in depth or magnitude. This type of interaction has been described by Porensky (2011) and may or may not be widespread. However, if future studies uncover additional evidence for emergent interactions, this type of interaction will be especially important because it is difficult to predict or model on the basis of single-edge patterns (Supporting Information).

Future Directions

By combining parameter-based measurement techniques (outlined above) with our conceptual framework and its associated vocabulary (Fig. 3), researchers can compare edge interaction results across multiple study systems, response variables, and landscape contexts. More studies in a variety of landscapes are needed to determine how common different types of edge interactions are and how edge interactions alter the ecology of patchy and fragmented landscapes. As more studies are completed, it may become possible to determine the average ecological effect of edge interactions (and compare this to the average ecological effect of single-edge effects) by comparing effect sizes across studies.

Given that 10 out of 11 published studies detected significant edge interactions, it is important to develop conservation approaches that acknowledge the potential for edge interactions in patchy landscapes. For example, when designing conservation reserves, biologists may want to consider (and test for) edge interactions that could substantially alter the functional roles of narrow corridors and convoluted patches. Similarly, research on fragmentation may benefit from assuming that increased fragmentation leads to more edge interaction. Existing work suggests that strengthening interactions are likely to be most common, although weakening and emergent interactions are also possible. Thus, even if empirical data are scarce, managers may be able to improve the accuracy of predictions concerning the effects of broad-scale land conversion by assuming that nearby edge effects will strengthen each other to some degree. After taking actions that change landscape configuration, managers could use long-term monitoring to test the accuracy of their assumptions about edge interaction. Finally, in many landscapes the edge effects of more than two patch types are likely to intersect and interact. Important simulation-based work is currently being done on this front (Li et al. 2007; LaCroix et al. 2008), and this is a critical priority for future empirical research.

Although our goal was to highlight the importance of edge interactions, we believe studies on single-edge effects are clearly useful and relevant for a variety of situations. Some landscapes are not patchy enough for edge interactions to play a major role. Moreover, good information about single-edge effects is a necessary ingredient for the detection of edge interactions.

As landscapes worldwide become more spatially complex due to anthropogenic changes, it is critical to understand when, how, and why edge effects vary on the basis of landscape context. Edge interaction represents an important but currently understudied component of edge-effect context dependence. We suggest that although edge interactions are rarely looked for, they may be common in fragmented and patchy landscapes. Edge interactions can take a number of different forms and are likely to complicate predictive modeling efforts and management decision making. Clear recognition and quantification of edge interactions will pave the way for a deeper understanding of landscape ecology, more accurate modeling of landscapes and reserves, and more effective management.

Acknowledgments

Members of Young Lab 2008–2011, M.L. Cadenasso, V. Eviner, and two anonymous reviewers provided helpful comments on the manuscript. Financial support was provided by a National Science Foundation (NSF) Graduate Research Fellowship and a NSF Doctoral Dissertation Improvement Grant (L.M.P.), and NSF Long-term Research in Environmental Biology DEB-08–16453 (T.P.Y.).

Supporting Information

Figures illustrating edge-effect parameters and arithmetically additive interactions (Appendix S1), detailed descriptions of the findings and biological consequences of the 11 published studies (Appendix S2), and hypothetical examples that illustrate different types of edge interactions (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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